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

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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

actually reflect an attentional-scout process related to the upcoming eye movement itself has been difficult. In particular, studies exploring these activations have either used exogenous cues (e.g., Wauschkuhn et al. 1998) or required target discrimination at the future gaze location (e.g., Gutteling et al. 2010). The exogenous cue approach entails substantial attentional capture at the future gaze location, whereas target-discrimination tasks tend to invoke attentional processes at the future gaze position that go beyond saccade initiation.

By employing a design that allowed the isolation of presaccadic electrophysiological activity independent of exogenous capture or additional task requirements at the future gaze location, we sought to investigate whether the recentering bias would be reflected in activity modulations solely related to guiding the eye movement toward a specific location. Specifically, we employed a centrally cued saccade paradigm with five positions along the horizontal meridian that enabled the comparison of centripetal recentering saccades to isoamplitude centrifugal saccades starting from the same fixation position and having identical directional probability (cf. Krebs et al. 2010a). In line with the commonly observed contralateral layout of attentional orienting and the anticipatory visual-field shifts observed in LIP neurons, our analysis aimed at identifying neural activity occurring contralateral to the direction of the upcoming saccade over posterior sites, thereby providing evidence for location-specific attentional shifts. Considering the unique target location of recentering saccades, along with the previously observed evidence for decreased SRTs, we hypothesized that such saccades would be associated with diminished attentional-shift activity, reflecting the preferential coding of the center of straight-ahead gaze.

MATERIALS AND METHODS

Participants and paradigm. Sixteen participants (mean ± SD age: 22 ± 2.6 yr; 10 men, 6 women) performed an endogenously cued saccade task while EEG was recorded from 64 scalp sites. All participants gave written informed consent before the experiment in accordance with the Duke Medical Center Institutional Review Board for human subjects. Participants were paid a total amount of $35 ($15/h).

We used a cued saccade paradigm that manipulated saccade direction (left vs. right) as well as the orientation of the saccade vector (centrifugal vs. centripetal) relative to the primary position (straight-ahead gaze; Fig. 1A). On each trial, based on a color cue presented at the currently foveated position, participants either performed a saccade to the left or right neighboring square or maintained fixation at the current position. At the beginning of each experimental run, participants saw an instruction screen that displayed the assignment of the color cues (e.g., green = right, red = left, blue = maintain fixation; counterbalanced across participants). These instructions were followed by the default stimulus display consisting of five white squares (each 0.5° × 0.5° of visual angle) on a black background, with the central square located at the center of the screen and with an even between-square spacing of 7° (Fig. 1A). We refer to the central position of these five locations as "position 0," the adjacent ones as "position 1" on the left or right, and the most eccentric ones as "position 2" on the left or right. At the start of each run, participants fixated the center square until a colored cue (duration 300 ms) appeared at that position, signaling to either execute the first 7° saccade to the adjacent square in the indicated direction or maintain fixation. For saccade trials, after the eye movement was performed, the participants' gaze remained at the new square until the next cue appeared at this newly foveated position. On maintain-fixation trials, the participants' gaze remained at the same square until another cue prompted the next eye movement. Saccade directions from all positions were randomized throughout each run, except from position 2 on the left and the right, which necessarily required a return to the neighboring, more medial, position 1. Participants were asked to execute each saccade as quickly and as accurately as possible and to minimize blinking. The

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. 1*B*), 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. 1*B*): 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. 1*C*). 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. 1*B*: 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. 2*A*). 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. 2*A*, *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. 2*B*). 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. 2*B*, *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

in occipital and parietal visual areas should precede the included saccades in either condition (cf. Lamme and Roelfsema 2000), thereby ruling out any significant differential contribution of the cue offset.

RESULTS

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 ~180 ms), followed by a later centro-parietal positivity (starting around ~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 ~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 ~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

the onset of a symbolic cue instructing participants to covertly shift their attention in space (Hopf and Mangun 2000). While the factor of contralaterality alone did not yield a significant effect in the respective rANOVA for the peak amplitude values at the collapsed PO7/PO8 electrodes (all *P* values > 0.09), we observed a significant interaction between contralaterality and saccade orientation between 320 and 360 ms after cue [320 to 340: $F_{(1,15)}$ = 4.69, *P* = 0.047; 340 to 360: $F_{(1,15)}$ = 6.01, *P* = 0.026], reflecting a slightly diminished contralateral negativity following cues that directed the gaze toward the primary position.

Presaccadic activity (saccade locked). The results of the saccade-locked analyses, collapsed across left and right saccade directions, are shown in Fig. 2*B*. Note that in this case neural activity was time-locked to saccade onset, requiring a baseline prior to the onset of the preceding cue (−800 to −600 ms). Because of the high variability in the SRTs, the cue-related ERP components were washed out in these saccade-locked averages, as would be expected. Both 1-to-2 centrifugal and 1-to-0 centripetal saccades starting at position 1 were associated with a positive deflection over central electrodes that started around 120 ms prior to the saccade and became stronger up to the onset of the eye movement at *time zero* (Fig. 2*B*, *top*). Analogous to the cue-locked analysis, none of the paired *t*-tests quantifying overall activity differences between the conditions of interest showed any significant differences between −60 and −20 ms over centro-parietal electrodes (Cz, CPz; all *P* values > 0.09; Fig. 2*B*, *bottom*).

Based on the notion that presaccadic attentional deployment would not only follow a contralateral mapping but would also likely be temporally closely linked to the onset of the saccade itself, we performed a rANOVA analogous to the cue-locked analysis above, i.e., combining leftward and rightward saccades to reflect contra- and ipsilateral activity relative to the saccade direction. The resulting topographic distributions are shown in Fig. 3*B* with contralateral activity represented over the left hemisphere and ipsilateral over the right. Consistent with our hypothesis, we observed a negative deflection contralateral to the future gaze location similar to that in the cue-locked analysis, albeit much stronger, starting at around −160 ms prior to the saccade onset and again focused over parietal/occipital recording sites. The respective rANOVA for the peak amplitude electrode PO3 yielded a highly significant main effect of contralaterality over the entire range between −100 and −20 ms [−100 to −80: $F_{(1,15)}$ = 10.04, *P* = 0.006; −80 to −60: $F_{(1,15)}$ = 12.95, *P* = 0.003; −60 to −40: $F_{(1,15)}$ = 16.19, *P* = 0.001; −40 to −20: $F_{(1,15)}$ = 12.28, *P* = 0.003]. Importantly, the observed presaccadic contralateral negativity appeared to be shorter in duration and weaker prior to centripetal recentering saccades (1-to-0) compared with centrifugal saccades starting from the same position 1 (1-to-2), suggesting a lower level of attentional shift activity prior to the former. Statistically, this modulation was reflected by a significant interaction of contralaterality and saccade orientation between −100 and −40 ms before saccade onset [−100 to −80: $F_{(1,15)}$ = 5.08, *P* = 0.039; −80 to −60: $F_{(1,15)}$ = 6.24, *P* = 0.025; −60 to −40: $F_{(1,15)}$ = 5.88, *P* = 0.028; −40 to −20: *P* > 0.2].

To rule out that this centrifugal-versus-centripetal differential pattern could have been mainly driven by differences in the SRT distribution relative to the cue offset at 300 ms, an analogous saccade-locked analysis was performed that only included trials with SRTs larger than 400 ms in both conditions. The main effect of contralaterality between −120 and −40 ms [−100 to −80: $F_{(1,15)}$ = 12.69, *P* = 0.003; −80 to −60: $F_{(1,15)}$ = 20.90, *P* < 0.001; −60 to −40: $F_{(1,15)}$ = 24.39, *P* < 0.001] and the accompanying interaction with saccade direction between −100 and −40 ms [−100 to −80: $F_{(1,15)}$ = 5.39, *P* = 0.035; −80 to −60: $F_{(1,15)}$ = 7.11, *P* = 0.018; −60 to −40: $F_{(1,15)}$ = 4.28, *P* = 0.056] were essentially preserved in this alternative analysis, ruling out that any possible interaction with cue offset contributed significantly to the initially observed pattern.

DISCUSSION

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

and the selection of specific locations in space across varying task requirements, thereby representing a shared mechanism between overt and covert attentional shifts (Corbetta et al. 1998).

Turning to the main focus of the present study, the contralateral presaccadic component described above was significantly diminished prior to recentering saccades, thereby paralleling the differential saccade latency patterns and supporting the view that the primary position is a preferentially coded location. From a behavioral perspective, the recentering bias has been linked to the dynamics of eye-head coordination in natural gaze shifts that combine eye and head movements. If the eye position is already deviated from the primary position in the direction of an upcoming gaze shift (ipsiversive), the head is usually moved to recenter the eyes before an even further saccade is initiated. In contrast, if the eye position is already deviated in the opposite direction of an upcoming gaze shift (contraversive), the eyes automatically counterrotate toward the primary position before any head movement is initiated, thereby resulting in faster saccade initiation (Fuller 1996). Neurally, in keeping with the view that the posterior presaccadic component is related to anticipatory visual-field shifts, the observed differential presaccadic modulation indicates that such shifts may occur more readily for saccades toward the primary position. Consistently, parietal neurons are known to play a role in the coordinate transformation between eye-centered and head-centered reference frames (Cohen and Andersen 2002), a process that requires information about relative orbital positions. The diminished activity over posterior regions prior to recentering compared with centrifugal saccades may thus reflect the reduced requirements for coding the primary position, in which the eye-centered and head-centered reference frames are perfectly aligned.

Such a mechanism likely relies on interactions with subcortical regions such as the SC (Fries 1984). In particular, the firing activity of a large portion of collicular neurons seems to be modulated by the position of the eyes (Campos et al. 2006; Pare and Munoz 2001; Van Opstal et al. 1995), and it is well known that eye and head position information are integrated in the SC (Kardamakis and Moschovakis 2009; Sparks 2002). In line with this notion, we recently found that recentering saccades are characterized by diminished neural activity in the human SC using fMRI (Krebs et al. 2010a). Despite this clear subcortical activity modulation, the fMRI measures in that study did not reveal significant recentering-related modulations in saccade-processing areas in the cortex. In light of the effects observed in the present EEG data, a plausible explanation for that result is that the presaccadic cortical modulations may be so transient that they were diluted in the fMRI study by neural processes that are common to all saccade types, e.g., cue interpretation and saccade execution processes, which cannot be easily separated with fMRI because of its low temporal resolution. In the present study, however, the much greater temporal resolution of the EEG measure made it possible to pin down these rather transient presaccadic attentional modulations from posterior cortical sources. Consistently, the presaccadic modulations in the present study were exclusively observed when comparing contralateral and ipsilateral activity with respect to saccade direction. In contrast, when comparing general direction-unspecific activity levels we found no significant differences between recentering and centrifugal saccades (Fig. 2), underscoring the location-specific nature of this presaccadic component.

It is important to consider some additional issues concerning the idea that the observed presaccadic posterior activity is indeed related to attentional guidance processes. First, it is important to consider the possibility that the differential presaccadic activity levels mainly arise from differences in the oculomotor setup, as the default position of the eyes puts minimal strain on the eye muscles, and therefore centrifugal saccades necessitate greater work against muscular force. However, several considerations would argue against a mere muscular explanation of the differential presaccadic effect observed here. First, the focal contralateral posterior distribution does not support the notion that this component reflects increased muscular effort for centrifugal saccades. Rather, increased muscular

resistance, and the associated activity in motoneurons innervating the extraocular muscles, would likely ramify in an anterior scalp distribution (Riemslag et al. 1988). Specifically, the saccadic spike potential would be expected to be strongest around the extraocular channels and extend gradually posteriorly (Keren et al. 2009; Thickbroom and Mastaglia 1985). Second, if the observed component did indeed reflect muscular effort, one would expect an increase until the onset of the saccade. In contrast, the differential effect in the present data started around 120 ms prior to the saccade and began to decrease at around 40 ms prior, confirming that the observed effect is independent of the saccadic spike potential. Finally, cortical regions may receive indirect information about the current muscular resistance from the SC. During the execution of an eye movement, a copy of the motor signal, the so-called corollary discharge, is conveyed to the FEF, which presumably helps to stabilize the visual input (Sommer and Wurtz 2004). Accordingly, differential modulations of this signal due to recentering would be expected to be observed over frontal sites, originating from FEF. Moreover, similar to the signal that actually drives the extraocular muscles, the neural activity related to the corollary discharge is thought to increase gradually until saccade onset (reviewed in Sommer and Wurtz 2008). Thus neither the posterior topographic distribution of the observed effect nor its time range seems to support a mere muscular resistance explanation.

Another alternative explanation for the differential pattern observed for centrifugal and centripetal saccades may be related to the saccade latency distribution relative to the offset of the cue stimulus. Given that centripetal saccades were associated with shorter latencies, a slightly greater number of those saccades were likely to start in temporal proximity to the cue offset at 300 ms. By performing an analogous saccade-locked analysis considering only saccades with latencies greater than 400 ms, we sought to rule out any significant contribution of the cue offset. Specifically, a minimum delay of 100 ms between cue offset and saccade onset was used to guarantee that the neural response to the cue offset mostly precedes the saccade onset in the posterior visual regions of interest (Lamme and Roelfsema 2000). In this analysis, the diminished contralateral activity preceding recentering compared with centrifugal saccades was preserved, indicating that the cue offset did not significantly contribute to the differential pattern.

The present study investigated the neural underpinnings of the presaccadic attentional deployment in relation to the saccadic recentering bias in humans. We observed a contralateral negative deflection within the last 100 ms prior to saccade onset over posterior sites, likely reflecting anticipatory attentional shifts toward the future gaze location arising from the parietal (and occipital) cortices. Importantly, this presaccadic enhancement was strongly attenuated prior to recentering saccades relative to isoamplitude centrifugal saccades from the same position, supporting the notion that the primary position requires less attentional guidance. From a more general perspective, such a mechanism might serve to facilitate the recentering of an observer's gaze to the default central position, enabling an efficient exploration of the visual world.

GRANTS

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: R.M.K., C.N.B., M.A.S., and M.G.W. conception and design of research; R.M.K. and H.H.Z. performed experiments; R.M.K. and H.H.Z. analyzed data; R.M.K., C.N.B., M.A.S., and

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.

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REFERENCES

Campos M, Cherian A, Segraves MA. Effects of eye position upon activity of neurons in macaque superior colliculus. J Neurophysiol 95: 505–526, 2006. [PubMed: 16192333]

Cavanagh P, Hunt AR, Afraz A, Rolfs M. Visual stability based on remapping of attention pointers. Trends Cogn Sci 14: 147–153, 2010. [PMCID: PMC2847621] [PubMed: 20189870]

Clementz BA, Brahmbhatt SB, McDowell JE, Brown R, Sweeney JA. When does the brain inform the eyes whether and where to move? An EEG study in humans. Cereb Cortex 17: 2634–2643, 2007. [PubMed: 17283204]

Cohen YE, Andersen RA. A common reference frame for movement plans in the posterior parietal cortex. Nat Rev Neurosci 3: 553–562, 2002. [PubMed: 12094211]

Cohen JY, Heitz RP, Schall JD, Woodman GF. On the origin of event-related potentials indexing covert attentional selection during visual search. J Neurophysiol 102: 2375–2386, 2009. [PMCID: PMC2775385] [PubMed: 19675287]

Colby CL, Duhamel JR, Goldberg ME. Oculocentric spatial representation in parietal cortex. Cereb Cortex 5: 470–481, 1995. [PubMed: 8547793]

Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL. A common network of functional areas for attention and eye movements. Neuron 21: 761–773, 1998. [PubMed: 9808463]

Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res 36: 1827–1837, 1996. [PubMed: 8759451]

Duhamel JR, Colby CL, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. Science 255: 90–92, 1992. [PubMed: 1553535]

Durand JB, Trotter Y, Celebrini S. Privileged processing of the straight-ahead direction in primate area V1. Neuron 66: 126–137, 2010. [PubMed: 20399734]

Evdokimidis I, Liakopoulos D, Papageorgiou C. Cortical potentials preceding centrifugal and centripetal self-paced horizontal saccades. Electroencephalogr Clin Neurophysiol 79: 503–505, 1991. [PubMed: 1721577]

Fries W. Cortical projections to the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. J Comp Neurol 230: 55–76, 1984. [PubMed: 6096414]

Fuller JH. Eye position and target amplitude effects on human visual saccadic latencies. Exp Brain Res 109: 457–466, 1996. [PubMed: 8817276]

Godijn R, Pratt J. Endogenous saccades are preceded by shifts of visual attention: evidence from cross-saccadic priming effects. Acta Psychol (Amst) 110: 83–102, 2002. [PubMed: 12005230]

Goldberg ME, Wurtz RH. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. J Neurophysiol 35: 560–574, 1972. [PubMed: 4624740]

Gutteling TP, van Ettinger-Veenstra HM, Kenemans JL, Neggers SF. Lateralized frontal eye field activity precedes occipital activity shortly before saccades: evidence for cortico-cortical feedback as a mechanism underlying covert attention shifts. J Cogn Neurosci 22: 1931–1943, 2010. [PubMed: 19702472]

Hopf JM, Luck SJ, Girelli M, Hagner T, Mangun GR, Scheich H, Heinze HJ. Neural sources of focused attention in visual search. Cereb Cortex 10: 1233–1241, 2000. [PubMed: 11073872]

Hopf JM, Mangun GR. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. Clin Neurophysiol 111: 1241–1257, 2000. [PubMed: 10880800]

Kardamakis AA, Moschovakis AK. Optimal control of gaze shifts. J Neurosci 29: 7723–7730, 2009. [PubMed: 19535584]

Keren AS, Yuval-Greenberg S, Deouell LY. Saccadic spike potentials in gamma-band EEG: characterization, detection and suppression. Neuroimage 49: 2248–2263, 2009. [PubMed: 19874901]

Klostermann W, Kompf D, Heide W, Verleger R, Wauschkuhn B, Seyfert T. The presaccadic cortical negativity prior to self-paced saccades with and without visual guidance. Electroencephalogr Clin Neurophysiol 91: 219–228, 1994. [PubMed: 7522151]

Kowler E, Anderson E, Dosher B, Blaser E. The role of attention in the programming of saccades. Vision Res 35: 1897–1916, 1995. [PubMed: 7660596]

Krebs RM, Schoenfeld MA, Boehler CN, Song AW, Woldorff MG. The saccadic re-centering bias is associated with activity changes in the human superior colliculus. Front Hum Neurosci 4: 193, 2010a. [PMCID: PMC2987555] [PubMed: 21103010]

Krebs RM, Woldorff MG, Tempelmann C, Bodammer N, Noesselt T, Boehler CN, Scheich H, Hopf JM, Duzel E, Heinze HJ, Schoenfeld MA. High-field fMRI reveals brain activation patterns underlying saccade execution in the human superior colliculus. PLoS One 5: e8691, 2010b. [PMCID: PMC2805712] [PubMed: 20084170]

Kusunoki M, Goldberg ME. The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. J Neurophysiol 89: 1519–1527, 2003. [PubMed: 12612015]

Lamme VA, Roelfsema PR. The distinct modes of vision offered by feedforward and recurrent processing. Trends Neurosci 23: 571–579, 2000. [PubMed: 11074267]

Laurutis VP, Robinson DA. The vestibulo-ocular reflex during human saccadic eye movements. J Physiol 373: 209–233, 1986. [PMCID: PMC1182533] [PubMed: 3489091]

Luck SJ. Cognitive and neural mechanisms of visual search. Curr Opin Neurobiol 4: 183–188, 1994. [PubMed: 8038574]

Luck SJ, Girelli M, McDermott MT, Ford MA. Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. Cogn Psychol 33: 64–87, 1997. [PubMed: 9212722]

Lynch JC, McLaren JW. Deficits of visual attention and saccadic eye movements after lesions of parietooccipital cortex in monkeys. J Neurophysiol 61: 74–90, 1989. [PubMed: 2918350]

McIlwain JT. Effects of eye position on saccades evoked electrically from superior colliculus of alert cats. J Neurophysiol 55: 97–112, 1986. [PubMed: 3512789]

Moore T, Chang MH. Presaccadic discrimination of receptive field stimuli by area V4 neurons. Vision Res 49: 1227–1232, 2009. [PMCID: PMC2724369] [PubMed: 18501949]

Pare M, Munoz DP. Expression of a re-centering bias in saccade regulation by superior colliculus neurons. Exp Brain Res 137: 354–368, 2001. [PubMed: 11355382]

Remington RW. Attention and saccadic eye movements. J Exp Psychol Hum Percept Perform 6: 726–744, 1980. [PubMed: 6449540]

Riemslag FC, Van der Heijde GL, Van Dongen MM, Ottenhoff F. On the origin of the presaccadic spike potential. Electroencephalogr Clin Neurophysiol 70: 281–287, 1988. [PubMed: 2458236]

Sommer MA, Wurtz RH. Brain circuits for the internal monitoring of movements. Annu Rev Neurosci 31: 317–338, 2008. [PMCID: PMC2813694] [PubMed: 18558858]

Sommer MA, Wurtz RH. What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. J Neurophysiol 91: 1381–1402, 2004. [PubMed: 14573558]

Sparks DL. The brainstem control of saccadic eye movements. Nat Rev Neurosci 3: 952–964, 2002. [PubMed: 12461552]

Stelmach LB, Campsall JM, Herdman CM. Attentional and ocular mechanisms. J Exp Psychol Hum Percept Perform 23: 823–844, 1997.

Tatler BW. The central fixation bias in scene viewing: selecting an optimal viewing position independently of motor biases and image feature distributions. J Vis 7: 1–17, 2007. [PubMed: 18217799]

Thickbroom GW, Mastaglia FL. Cerebral events preceding self-paced and visually triggered saccades. A study of presaccadic potentials. Electroencephalogr Clin Neurophysiol 62: 277–289, 1985. [PubMed: 2408874]

van der Lubbe RH, Neggers SF, Verleger R, Kenemans JL. Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. Brain Res 1072: 133–152, 2006. [PubMed: 16427618]

Van Opstal AJ, Hepp K, Suzuki Y, Henn V. Influence of eye position on activity in monkey superior colliculus. J Neurophysiol 74: 1593–1610, 1995. [PubMed: 8989396]

van Velzen J, Eimer M. Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. Psychophysiology 40: 827–831, 2003. [PubMed: 14696736]

Walker R, Walker DG, Husain M, Kennard C. Control of voluntary and reflexive saccades. Exp Brain Res 130: 540–544, 2000. [PubMed: 10717796]

Wauschkuhn B, Verleger R, Wascher E, Klostermann W, Burk M, Heide W, Kompf D. Lateralized human cortical activity for shifting visuospatial attention and initiating saccades. J Neurophysiol 80: 2900–2910, 1998. [PubMed: 9862894]

Woodman GF, Kang MS, Rossi AF, Schall JD. Nonhuman primate event-related potentials indexing covert shifts of attention. Proc Natl Acad Sci USA 104: 15111–15116, 2007. [PMCID: PMC1986621] [PubMed: 17848520]

Wright RD, Ward LM. Orienting of Attention. New York: Oxford Univ. Press, 2008, p. 304.

Wurtz RH, Albano JE. Visual-motor function of the primate superior colliculus. Annu Rev Neurosci 3: 189–226, 1980. [PubMed: 6774653]

Figures and Tables

Fig. 1.
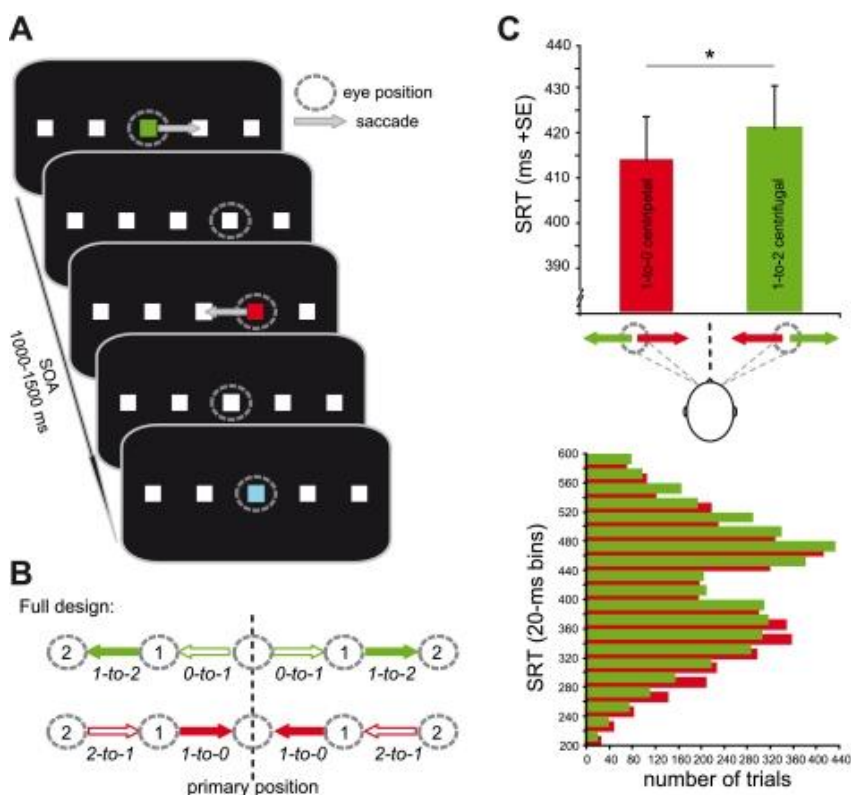
Paradigm and behavioral results. *A*: participants performed saccades from square to square along the horizontal meridian guided by instructional color cues. The color cues (300-ms duration), which appeared at the currently foveated square, signaled the direction of the next saccade (e.g., green = right 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*.

Fig. 2.
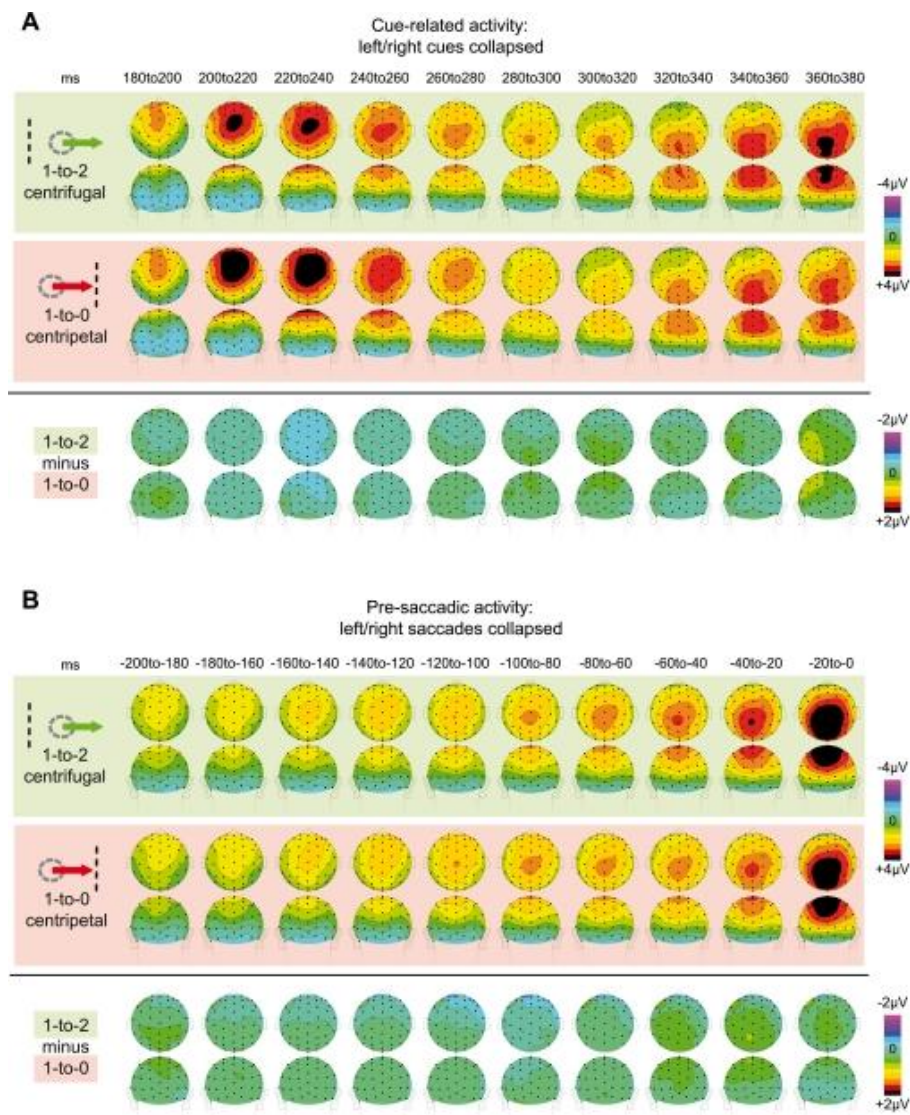
Averaged cue-locked and saccade-locked activity. *A*: scalp distributions for cue-locked activity were averaged across left/right cues for the conditions of interest (1-to-2 centrifugal and 1-to-0 centripetal), as well as for the difference between the two conditions, displayed between 180 and 380 ms after cue. *B*: an analogous analysis is shown for the saccade-locked data within a time range of −200 to 0 ms prior to saccade onset.

Fig. 3.
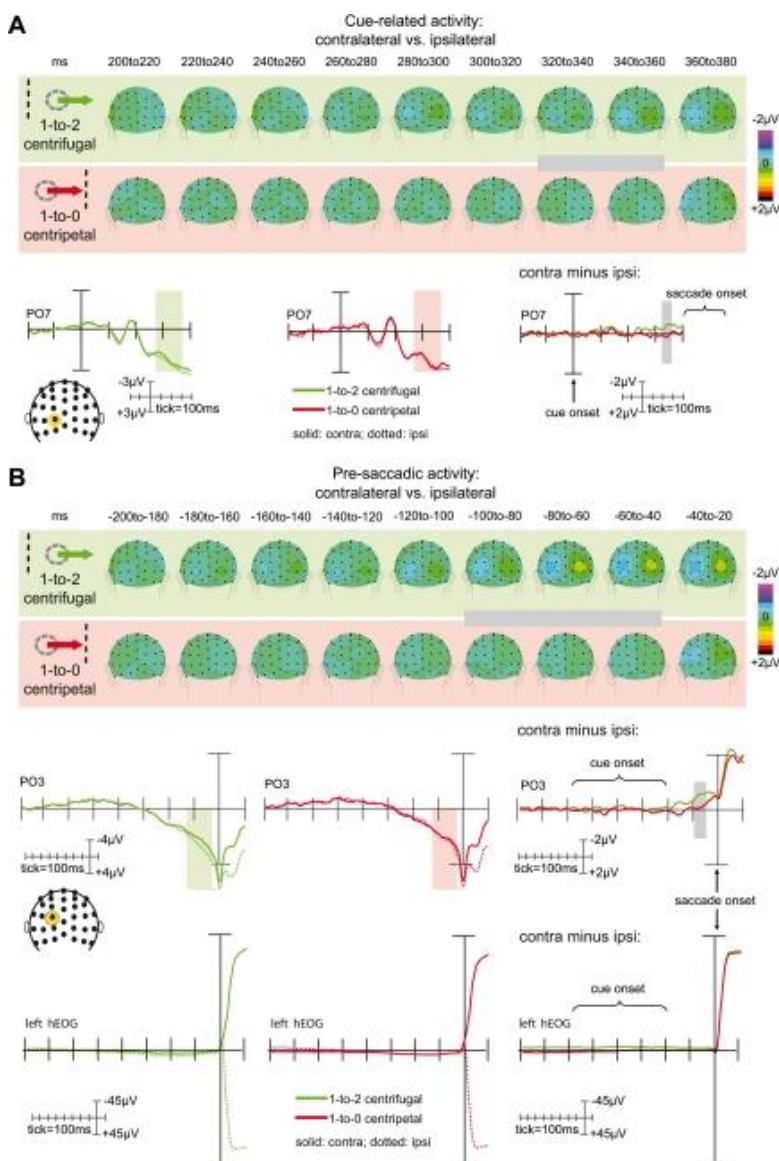
Contralateral activity enhancement. *A*: cue-locked scalp distributions were averaged to represent contra- and ipsilateral activity relative to the direction indicated by the cue for 1-to-2 centrifugal and 1-to-0 centripetal saccades. Contralateral negative deflections are displayed over the left hemisphere (with ipsilateral inverse deflections over the right hemisphere). Contralateral and ipsilateral event-related potential (ERP) traces, along with the respective difference wave (contra minus ipsi), are displayed separately for 1-to-2 centrifugal (depicted in green) and 1-to-0 centripetal (depicted in red) saccades. The contralateral negativity was diminished for cues preceding centripetal saccades between 320 and 360 ms after cue (indicated by gray bar). *B*: the analogous topographic distributions and activity traces are shown time-locked to saccade onset, revealing a robust presaccadic contralateral negativity. Centripetal saccades were again associated with reduced contralateral negativity compared with centrifugal saccades from the same position between −100 and −40 ms prior to saccade onset (indicated by gray bar). Horizontal electrooculogram (EOG) traces confirm that the observed posterior modulations occur well before the actual eye movement [contralateral vs. ipsilateral activity displayed over the left hemisphere (h)EOG].