RESEARCH ARTICLE | *The Role of Eye Movements in Perception, Cognition, and Action*

Perisaccadic perceptual mislocalization is different for upward saccades

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Grujic N, Brehm N, Gloge C, Zhuo W, Hafed ZM. Perisaccadic perceptual mislocalization is different for upward saccades. *J Neurophysiol* 120: 3198–3216, 2018. First published October 17, 2018; doi:10.1152/jn.00350.2018.—Saccadic eye movements, which dramatically alter retinal images, are associated with robust perimovement perceptual alterations. Such alterations, thought to reflect brain mechanisms for maintaining perceptual stability in the face of saccade-induced retinal image disruptions, are often studied by asking subjects to localize brief stimuli presented around the time of horizontal saccades. However, other saccade directions are not usually explored. Motivated by recently discovered asymmetries in upper and lower visual field representations in the superior colliculus, a structure important for both saccade generation and visual analysis, we observed significant differences in perisaccadic perceptual alterations for upward saccades relative to other saccade directions. We also found that, even for purely horizontal saccades, perceptual alterations differ for upper vs. lower retinotopic stimulus locations. Our results, coupled with conceptual modeling, suggest that perisaccadic perceptual alterations might critically depend on neural circuits, such as superior colliculus, that asymmetrically represent the upper and lower visual fields.

NEW & NOTEWORTHY Brief visual stimuli are robustly mislocalized around the time of saccades. Such mislocalization is thought to arise because oculomotor and visual neural maps distort space through foveal magnification. However, other neural asymmetries, such as upper visual field magnification in the superior colliculus, may also exist, raising the possibility that interactions between saccades and visual stimuli would depend on saccade direction. We confirmed this behaviorally by exploring and characterizing perisaccadic perception for upward saccades.

foveal magnification; perceptual stability; perisaccadic spatial remapping; saccadic compression; superior colliculus

INTRODUCTION

Saccades are instrumental for rapidly allocating foveal visual processing resources to interesting scene locations. However, each saccade introduces spurious shifts in retinal images, which normally go perceptually unnoticed, and the mechanisms underlying such perceptual stability are an active area of research (Bremmer et al. 2009; Brenner et al. 2008; De Pisapia et al. 2010; Duhamel et al. 1992; Hafed 2013; Hafed et al. 2015; Maij et al. 2010, 2011; Rao et al. 2016; Richard et al. 2009; Ross et al. 2001; Sommer and Wurtz 2008; Watson and Krekelberg 2009; Wurtz 2008; Wurtz et al. 2011; Ziesche and Hamker 2014; Zirnsak and Moore 2014).

Experimentally, perceptual stability mechanisms are studied by perisaccadically presenting briefly flashed visual stimuli (Ross et al. 2001). If saccades are associated with retinal and/or extraretinal mechanisms for handling saccade-induced retinal image disturbances, then perception of such brief flashes may be altered. The flashes effectively allow capturing momentary "snapshots" of the state of the visual system around the time of saccades. In cases with sufficiently low-contrast flashes, these flashes may go completely unnoticed in the phenomenon of "saccadic suppression" (Beeler 1967; Burr et al. 1994; Chen and Hafed 2017; Diamond et al. 2000; Hafed and Krauzlis 2010; Zuber and Stark 1966), which has its own rich set of properties and unsolved questions (Bellet et al. 2017; Benedetto and Morrone 2017; Bremmer et al. 2009; Chen and Hafed 2017; Crevecoeur and Kording 2017; Hafed and Krauzlis 2010; Krekelberg 2010; Zanos et al. 2016). However, with sufficiently visible flashes, even though such flashes are easily detected, their locations are grossly misestimated (perisaccadic perceptual mislocalization) (Cai et al. 1997; Honda 1989; 1991; Lappe et al. 2000; Maij et al. 2010; Morris et al. 2012; Ross et al. 1997; Zirnsak et al. 2014). Under conditions of bright illumination, misestimates of flash location appear as if the flashes are perceptually compressed toward the saccade target (Lappe et al. 2000; Ross et al. 1997), and it is this "perceptual compression" that we sought to explore.

Compression was initially studied along only one dimension and with horizontal saccades (Ross et al. 1997). Subjects made large horizontal eye movements, and flashes could appear along the same direction of the eye movements at either farther or nearer eccentricities than the saccade target. Perisaccadic flashes were perceptually compressed toward the saccade target such that flashes more eccentric than the target were mislocalized backward in a direction opposite to the saccade direction and flashes less eccentric were mislocalized forward. Subsequent studies explored two-dimensional patterns of compression with flashes off the axis of the saccade (Kaiser and

Lappe 2004) and discovered asymmetries in two-dimensional compression as a function of flash eccentricity. Although the mechanisms behind these asymmetries are not fully understood, existing models agree that they may reflect interactions between oculomotor signals associated with saccade generation, on the one hand, and visual signals associated with flash locations, on the other, and, critically, in sensory and motor neural maps that exhibit "foveal magnification" (i.e., more neural tissue dedicated to central than peripheral visual field eccentricities) (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010).

In this study, we explored this idea further by asking whether perisaccadic perceptual mislocalization depends on movement direction. Prior experiments, exploring rightward and downward saccades (Kaiser and Lappe 2004; Ross et al. 1997; Zimmermann et al. 2015), did not reveal significant differences in mislocalization patterns as a function of saccade direction. However, our goal was to investigate this question in more detail, and for upward saccades in particular. We were specifically motivated by the notion that if perceptual mislocalization arises as a result of foveal magnification in sensory-motor maps, then other patterns of neural tissue magnification might dictate asymmetries in the patterns of perisaccadic perceptual mislocalization. For example, if the superior colliculus (SC), as a visual and saccade-related structure (Basso and May 2017; Gandhi and Katnani 2011; Sparks and Mays 1990; Veale et al. 2017; Wurtz 1996), were to be involved in perceptual effects associated with mislocalization (Hafed 2013; Richard et al. 2009; Veale et al. 2017), then this structure's putative magnification of upper visual field representations (Hafed and Chen 2016) might mean that mislocalization would be different for upward saccades. If so, this would provide important constraints on neural loci and mechanisms for such a highly robust perceptual phenomenon and would therefore more generally have strong implications on our understanding of perceptual stability in the face of continuous eye movements.

MATERIALS AND METHODS

Subjects. We recruited seven subjects (3 female; 21–42 yr old) in our main experiment using cardinal saccade directions (e.g., see Fig. 1 and *Behavioral tasks*). We then recruited six subjects (2 women) for a second experiment involving oblique saccades (e.g., see Fig. 9 and *Behavioral tasks*). Two of the subjects (1 female) participated in both experiments. All subjects provided informed, written consent in accordance with the Declaration of Helsinki, and the experiments were approved by ethics committees at Tübingen University. Each subject completed five sessions of 1.5 h each in the first experiment, with each session consisting of four blocks of 160 trials per block. Because the second experiment had fewer conditions (only 2 saccade directions instead of 4), the subjects required only two to three sessions each.

Laboratory setup. The laboratory setup was similar to that described previously (Bellet et al. 2017; Hafed 2013; Tian et al. 2016). Briefly, subjects sat in a dark room in front of a display running at 85 Hz and spanning $34.1° \times 25.9°$. Stimuli were white (97.3 cd/m^2) and presented over a uniform gray background (20.5 cd/m^2). Head fixation was achieved using a custom-made chin-and-forehead rest described previously (Hafed 2013), and we tracked eye movements using a video-based eye tracker running at 1 kHz (EyeLink 1000; SR Research). Subjects indicated their perceived flash location (see *Behavioral tasks*) by pressing a computer mouse button after moving the mouse pointer to the desired point on the display. We used the

Psychophysics Toolbox (Brainard 1997; Kleiner et al. 2007; Pelli 1997) for real-time display control.

Behavioral tasks. In the main experiment with cardinal saccade directions (e.g., see Fig. 1), trials started with the onset of a white fixation spot of ~7.3 $\times$ 7.3 min arc dimensions. The spot appeared ~7.3° from the center of the display in one of the four cardinal directions (right, left, up, or down relative to display center), and it was then jumped by ~14.6° in the opposite direction after 1–3 s. That is, if the spot appeared ~7.3° to the right of display center at trial onset, it jumped to ~7.3° to the left of display center after 1–3 s, and similarly for the other initial fixation spot locations. In all cases, the fixation spot jump was the cue to generate a visually guided saccade (~14.6° in amplitude), as quickly as possible, from the old spot location to its new one. We started trials with the fixation spot being displaced from display center because we wanted to employ fairly large saccades (~14.6° in amplitude) for all saccade directions, which would have been impossible for vertical saccades using our display's aspect ratio. The use of relatively large saccades was instrumental to allow us to compare our observations with those in classic investigations of perisaccadic perceptual mislocalization, in which large saccades were also used (Cai et al. 1997; Kaiser and Lappe 2004; Ross et al. 1997, 2001).

In every trial, a white square of ~0.73° $\times$ 0.73° dimensions was flashed for only one display frame (~12 ms) after one of five different latencies from the fixation spot jump (~60, 106, 153, 212, or 259 ms). Given that our observed saccadic reaction times were typically >100 ms and <300 ms, this meant that relative to saccade onset, the flash could come either before, during, or after an eye movement (with a relatively uniform distribution), allowing us to map time courses of perisaccadic percepts. After a short delay from the flash presentation (500 ms), a mouse pointer was made visible always in the center of the display, and subjects were asked to click (within <3,500 ms) on the location where they saw the flash. If subjects did not see any flash, they were instructed to click at the center of the display, but this event was rare (only 1.38% of accepted trials had a click near the center of the display). Subjects were otherwise encouraged to localize the flash accurately rather than making speeded clicks (manual reaction times were 1,241 $\pm$ 347 ms, mean $\pm$ SD; median: 1,174 ms).

The flash could appear centered on one of eight possible equally spaced positions around a virtual circle surrounding the saccade target position (e.g., see Fig. 1). This virtual circle had a radius of ~3.6°. In other words, if the fixation spot jumped to a new location, instructing a saccade, the flash could appear at an eccentricity of ~3.6° from the new fixation spot location in one of eight equally spaced directions. Because prior experiments have revealed that two-dimensional patterns of perisaccadic mislocalization depend on flash eccentricity relative to saccade target eccentricity (Kaiser and Lappe 2004), we always labeled flash positions during our analyses by using a relative numbering convention, regardless of saccade direction. Specifically, *flash 1* was always the flash along the saccade direction and farther away from initial fixation than the saccade target. *Flashes 2–8* were then the successive flashes along the virtual circle if one were to traverse this circle in a clockwise manner (e.g., see Fig. 1). Thus, with the use of this convention, *flashes 1*, *2*, and *8* were always the flashes that were more eccentric than the saccade target position relative to initial fixation position before the saccade, and *flashes 4*, *5*, and *6* were always the flashes that were closer to initial fixation than the saccade target. Similarly, *flashes 2*, *4*, *6*, and *8* were always the flashes for which both "parallel" and "orthogonal" mislocalizations relative to the vector of the saccade (e.g., see Figs. 1 and 6*A*) could occur (Kaiser and Lappe 2004).

In our second experiment, we had subjects perform 45-deg oblique saccades. The subjects made either rightward-upward or rightward-downward saccades. The start and end points of the fixation spot (relative to display center) were adjusted accordingly such that saccade amplitude was similar to the cardinal saccade direction experiment described above (~14.6°). Also, the displacement of the fixation

spot position from display center before and after the saccade was always symmetric relative to display center, exactly as in the first experiment above. Finally, flash times and locations relative to the saccade target location and saccade direction vector, as well as all flash numbering and naming conventions, were identical to those described above.

Data analysis. We detected saccades using eye velocity and acceleration criteria (Chen and Hafed 2013), and we manually inspected all detected movements. We identified the saccade of interest (i.e., the movement responding to the jump in fixation spot location), and we analyzed its associated percepts. We excluded from analyses all trials in which a blink or microsaccade occurred between −200 ms from saccade target jump until the saccade was executed. We also excluded trials with saccade reaction times <100 ms or >500 ms from the jump in fixation spot, as well as trials with saccade end points being >4.5° from the saccade target (e.g., see Fig. 5, *A* and *B*), to ensure that subjects made appropriate target-directed movements. Because of variability in saccade metrics for upward vs. downward saccades (Hafed and Chen 2016), in other analyses, we only included saccades with end points overlapping with end points of movements of saccades made in all other directions (e.g., see Fig. 5). In other words, we only considered saccades with "overlapping" end points across all executed saccade directions. This allowed us to establish that changes in mislocalization patterns for, say, upward saccades (e.g., see Figs. 1–4) were not explained by variability in the metrics of the saccades themselves when compared with other saccade directions. We also explicitly tested for effects of saccade amplitude on mislocalization. Finally, we excluded any trials with percept reports (i.e., mouse button press locations) within a square of ±2.44° × ±2.44° from display center or with percept (manual) reaction times >3,500 ms. These were trials in which subjects likely did not see the flash at all, perhaps due to blinks and other lapses. In total, we had 17,454 acceptable trials from the first experiment, of which 14,766 could be used in the more stringent overlapping end points control analyses. For the second experiment (with fewer conditions), the trial numbers were 6,995 and 6,253, respectively.

We measured perceived flash location as a function of saccade direction and flash time relative to saccade onset. We defined a perisaccadic interval of interest in primary analyses as the interval in which flash times occurred 0–50 ms after saccade onset, because this is typically when maximal mislocalization is expected to occur, but we also saw mislocalization in other intervals by plotting the full time courses of mislocalization (e.g., see Figs. 4, 6, 8, and 11). We also compared this interval of interest with a presaccadic baseline interval with flash times occurring between −125 and −75 ms relative to saccade onset. To obtain time courses of percepts (e.g., see Fig. 4), we binned flash times relative to saccade onset in 50-ms bins, and we stepped the binning windows in steps of 2 ms. To display a spatial trajectory of perceived flash locations, we plotted all time-course points in an interval around saccade onset (e.g., −100 to +100 ms) as spatial coordinates (e.g., vertical perceived position vs. horizontal perceived position). The trajectories typically started from a baseline perceived position, then moved closer toward the saccade target location, and then relaxed back to near the original perceived position (e.g., see Figs. 6*A*, 8*A*, 8*B*, and 9*D*; also see Supplemental Video S1, available in the data supplement online at the *Journal of Neurophysiology* Web site). Therefore, the trajectories of percepts made a loop in position space. We estimated the direction of mislocalization by creating a vector whose origin was the midpoint of percepts at −100 or +100 ms relative to saccade onset (i.e., the baseline percept) and whose end point was the point of either maximal orthogonal or parallel mislocalization (depending on the specific goal of a given analysis) between −100 and +100 ms from saccade onset (typically occurring somewhere in the interval from 0 to 50 ms after saccade onset).

To compare perceptual mislocalization for different saccade directions, we rotated all data to align with a rightward saccade. For

example, for an upward saccade, we rotated all data 90° clockwise to facilitate comparison with rightward saccades. All flash locations relative to the saccade target and initial fixation position were consistently rotated as in the scheme of Fig. 1. This was critical to maintain relative eccentricity relationships for all flash locations across saccade directions, especially because it was previously suggested that it is relative eccentricity that seems to matter the most for patterns of two-dimensional perisaccadic mislocalization (Kaiser and Lappe 2004; VanRullen 2004). Thus we reported two-dimensional percept position in terms of position parallel to the saccade direction vector and position orthogonal to the saccade direction vector (e.g., see Fig. 6*A*).

All figures in this paper report the numbers of trials used for the analyses, as well as measures of variability in the form of either standard error bars (SE) or 95% confidence intervals. Because perisaccadic mislocalization is a highly robust phenomenon (Ross et al. 1997), with many replications in the field over at least two decades, we pooled data from all subjects for most of our analyses. Because the number of trials collected per subject was matched across individuals (see *Subjects*), and because data exclusions described above (e.g., blinks or lapses) were not expected to be strongly biased across conditions and subjects, no single subject or subset of subjects dominated the results from the pooled data. To support this assertion, we also confirmed that all of our key observations can be made at the individual subject level (e.g., Figs. 3, 4, 7, and 10 show all the key results from both experiments in each individual subject that we recruited).

Finally, for conceptual modeling, we asked whether a simple mechanism of saccade-induced translation of visual location of stimuli, but in neural tissue coordinates, can account for perceptual mislocalization (VanRullen 2004). The specific question that we asked was whether possible asymmetries in tissue representations between the upper and lower visual fields are sufficient to make upward saccades look like outliers in terms of perceptual mislocalization. As such, we modeled visuomotor maps as having both foveal magnification, as in VanRullen (2004), as well as upper vs. lower visual field asymmetries, as in Hafed and Chen (2016). The equations for the maps with upper and lower visual field asymmetries were identical to those in Hafed and Chen (2016). The equations for perfectly symmetric maps were similar, but without the area scale factor invoked in Hafed and Chen (2016). Note that these maps were based on prior descriptions of SC topography, but their mathematical form is identical to other visual maps in the brain (e.g., primary visual cortex, V1). Specifically, the maps employ logarithmic warping such that foveal visual image locations are associated with a greater area of neural tissue. Naturally, maps mathematically fit to the size of V1 or other visual or motor areas can be potentially used, but our goal was to conceptually ask whether asymmetries in maps between upper and lower visual field representations can be related to our experimental results. Thus specific map parameters (fit to V1 or SC or elsewhere) are less critical than the idea that a map may or may not have upper and lower visual field asymmetries.

RESULTS

We ran seven human participants on an experiment involving brief stimulus flashes presented around the time of either rightward, leftward, downward, or upward saccades. Subjects localized the flashes at the ends of trials by manually pointing a cursor to where they perceived them. Flashes could occur from approximately −100 to approximately +100 ms from saccade onset, and with roughly uniform probability (see MATERIALS AND METHODS).

We first replicated observations of two-dimensional perisaccadic perceptual mislocalization for rightward saccades (Kaiser and Lappe 2004). In our experiment, a brief flash could appear at any one of eight possible locations lying on a virtual circle

surrounding the saccade target (Fig. 1*A*, *top*). Because mislocalization patterns depend on flash eccentricity from initial fixation position relative to saccade target eccentricity (Kaiser and Lappe 2004; VanRullen 2004), we classified flashes as being either more ("farther") or less ("nearer") eccentric than the saccade target (relative to initial fixation), using the numbering convention shown in Fig. 1*A*, *top*. Thus *flashes 1, 2*, and *8* were all farther from initial fixation than the saccade target and were therefore expected to be misperceived backward (Kaiser and Lappe 2004); *flashes 4*, *5*, and *6* were nearer to initial fixation and were expected to be misperceived forward (Kaiser and Lappe 2004). The net result is a "compression" of percepts toward the saccade target as shown in Fig. 1*A*, *bottom*. Here, each data point indicates average perceived location for flashes presented 0–50 ms from saccade onset, and each line connects each data point to its corresponding percept when flashes were presented ~100 ms before saccade onset (see MATERIALS AND METHODS) (i.e., when perception was expected to be more veridical). Two-dimensional compression of perceived flash location took place (Kaiser and Lappe 2004).

For upward saccades (Fig. 1*B*), notable differences were evident to us and are the primary focus here. For example, with the use of the same conventions as in Fig. 1*A*, *flash 1* for upward saccades (Fig. 1*B*, *top*) was more eccentric than the saccade target relative to initial fixation position (Fig. 1*A*, *top*).

However, the perisaccadic percept associated with this flash location was significantly closer to the saccade target than for rightward saccades (Fig. 1*B*, *bottom*, with the percept being practically exactly at the saccade target location). In other words, at the time of expected peak mislocalization relative to saccade onset (0–50 ms from saccade onset), mislocalization for *flash 1* (and *flashes 2* and *8*) was stronger for upward saccades than for rightward ones (compare Fig. 1, *A* and *B*). In what follows, we quantify this and other differences in two-dimensional perisaccadic perceptual mislocalization patterns between upward saccades and other cardinal saccade directions, and we then explore potential origins and consequences of such differences.

Stronger compression of farther flash locations for upward saccades. Using the same numbering convention of flash locations as in Fig. 1, we compared perisaccadic perceptual mislocalization patterns for different saccade directions using a single reference frame (namely, flash eccentricity relative to saccade target eccentricity). This is because accounts of perisaccadic mislocalization critically rely on relative eccentricities of flashes and saccade targets (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010). In Fig. 2*A*, we plotted perceived flash location (relative to the saccade target) for all flashes occurring 0–50 ms from saccade onset, and we connected all data points
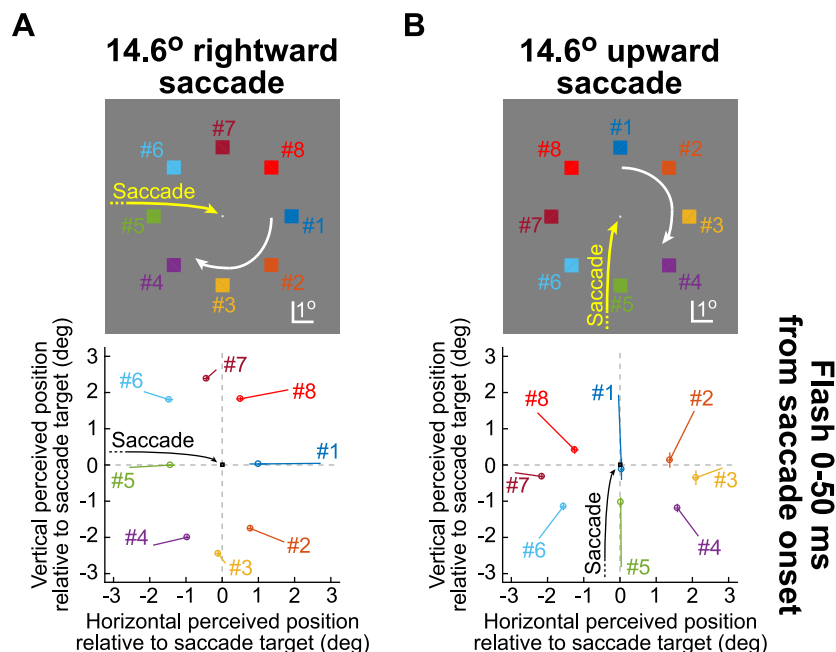

Fig. 1. Patterns of perisaccadic perceptual mislocalization for rightward vs. upward saccades. *A*, *top*: a schematic of our conventions for relating flash location to saccade direction. The yellow arrow indicates a rightward saccade toward the small white target presented in the middle of the schematic; the colored numbered squares indicate the possible perisaccadic brief flash locations relative to the saccade target. For example, *flash 1* indicates that a brief white flash appeared along the axis of the saccade direction and more eccentric than the saccade target (relative to initial fixation), and similarly for the other flashes (see MATERIALS AND METHODS). Flash locations were numbered in a clockwise manner indicated by the white circular arrow. *A*, *bottom*: graph shows the perceived position of each flash location (relative to the saccade target location) for flashes occurring 0–50 ms from saccade onset. Error bars denote SE across trials. Each data point is depicted at the end of a line whose other end point indicates the perceived position of the same flash when it occurred 75–125 ms before saccade onset: perisaccadic flashes were perceived as compressed toward the saccade target compared with the percept a long time before the saccade, as observed previously ($n = 80$–97 trials per flash location in the interval 0–50 ms from saccade onset, and $n = 80$–103 trials per flash location in the interval 75–125 ms before saccade onset). *B*, *top*: the same analysis in *A*, applied for upward saccades. The numbering conventions for flash locations relative to saccade target location and saccade direction are identical to those in *A*. *B*, *bottom*: graph shows that upward saccades were also associated with perisaccadic compression, but that the compression effect was markedly stronger than in *A*. For example, *flashes 1*, *2*, and *8* were associated with a closer perceived position to the saccade target than for rightward saccades (further illustrated and quantified in other figures). Note also that the starting position of the line for *flash 1* was already slightly closer to the saccade target than for rightward saccades, indicative of an initial bias in the percept (as discussed in more detail in Fig. 6*B*) ($n = 62$–95 trials per flash location in the interval 0–50 ms from saccade onset, and $n = 86$–112 trials per flash location in the interval 75–125 ms before saccade onset).

Fig. 2. Perisaccadic mislocalization was strongest for upward saccades with flash locations farther away from the saccade target location relative to initial fixation. *A*: for flashes occurring 0–50 ms from saccade onset, the perceived position of each flash is plotted relative to the saccade target location (similar to Fig. 1), but for each of the 4 cardinal saccade directions. The data were rotated such that the saccade vector in this figure was always rightward (despite the different saccade directions in the real experiment), but the relative positions of the flashes to the saccade vector in the rotation were maintained such that *flashes 1, 2,* and *8* were always the flashes that were farther away from the saccade target and *flashes 4, 5,* and *6* were always the flashes that were nearer than the saccade target (relative to initial fixation). Each solid line indicates the percepts associated with a given saccade direction according to the colored arrows, and error bars denote SE. The color coding of individual flash positions maintains the conventions set in Fig. 1. As can be seen, perisaccadic percepts for upward saccades (magenta) were an outlier from all other saccade directions: *flashes 1, 2,* and *8* were significantly more compressed toward the saccade target ($n = 698, 673, 669,$ and 652 saccades for rightward, leftward, downward, and upward saccades, respectively, roughly equally divided across all flash locations). *B*: for *flashes 1, 2,* and *8* (i.e., farther than the saccade target), we plotted the component of perceived flash position along the saccade direction (i.e., the *x*-axis values from *A*) for all 4 cardinal saccade directions. Upward saccades were associated with the strongest perisaccadic compression toward the saccade target (i.e., the smallest values of perceived position relative to saccade target location; black arrow). Error bars denote SE. *C* and *D*: similar analyses for flash times longer after saccade onset, demonstrating that the stronger mislocalization for upward saccades lingers for a longer time than in all other saccade directions ($n = 671, 762, 494,$ and 549 saccades for rightward, leftward, downward, and upward saccades, respectively, roughly equally divided across all flash locations). *E*: an analysis similar to that in *B* but for all flashes nearer to initial fixation than the saccade target (*flashes 4, 5,* and *6*; see schematic in the *inset*). The *y*-axis shows perceived position of the flashes (relative to the saccade target location) along saccade direction for all flashes occurring 0–50 ms from saccade onset. Unlike for flashes farther away from fixation (*B*), upward saccades showed levels of compression along the saccade direction vector similar to those of all other cardinal saccade directions (i.e., upward saccades were not an outlier) ($n = 253, 255, 246,$ and 251 trials for rightward, leftward, downward, and upward saccades, respectively).
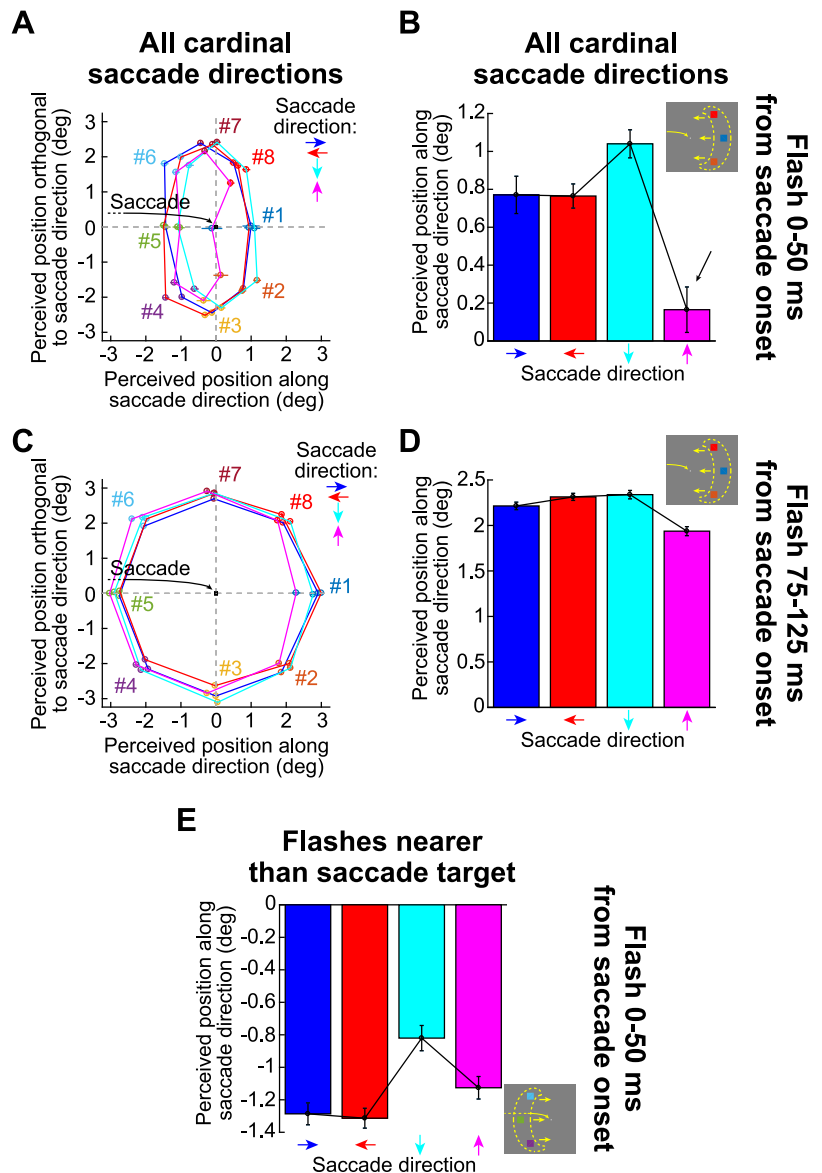
from all eight flash locations for a given saccade direction with a contour having a single color (4 colors denote the 4 saccade directions). To facilitate comparison of perisaccadic mislocalization for all saccade directions, we rotated all data points to align with the rightward saccade, and flash locations were also rotated to respect the conventions of Fig. 1 (see MATERIALS AND METHODS). For example, regardless of saccade direction, *flash 1* was more eccentric than the saccade target and along the vector of the saccade (parallel to the saccade vector), and *flash 5* was less eccentric and similarly along the vector of the saccade; on the other hand, *flash 2* was more eccentric than the saccade target, but at a clockwise-shifted angle relative to *flash 1* (i.e., having a component of position orthogonal to the saccade vector), and so on for all other flash locations. If perception was veridical, then the shown data points should all lie on a circle (e.g., Fig. 1*A, top*). However, percepts were compressed toward the saccade target. Critically, percepts for upward saccades were clear outliers compared with all other saccade directions: perceived flash position along the saccade direction vector for *flashes 1, 2,* and *8* was closer to the saccade target

location (i.e., closer to 0 on the *x*-axis) for upward saccades than for all other saccade directions. This means that there was stronger compression along the saccade direction for flashes farther away from the initial fixation position than the saccade target.

To summarize this observation, we plotted average perceived position parallel to the saccade vector for *flashes 1, 2,* and *8* (i.e., all flashes farther away from initial fixation than the saccade target). For flashes 0–50 ms after saccade onset (Fig. 2*B*), such perceived position was similar for rightward, leftward, and downward saccades, but upward saccades were associated with stronger compression (i.e., smaller values of perceived position along the saccade vector) ($P = 5.05 \times 10^{-10}$, 1-way ANOVA). Thus backward compression of flashes farther than the saccade target was stronger in perisaccadic intervals for upward saccades than for the other three saccade directions.

At longer time after saccade onset (e.g., ~100 ms), percepts of flash location were more veridical (i.e., recovered relative to Fig. 2*B*), as expected (Fig. 2*C*), but the outlying nature of

upward saccades still persisted even at such longer times (Fig. 2D) ($P = 2.28 \times 10^{-10}$, 1-way ANOVA). In other words, percept locations were closer to the real flash locations, but the recovery for upward saccades was less complete than for the other saccade directions. This might indicate that the time course of recovery after upward saccades might be slightly different compared with that for other movement directions. This outlying nature of upward saccades was also specific for flashes more eccentric than the saccade target. When we repeated the same analysis of Fig. 2B but for *flashes 4, 5, and 6* (i.e., nearer to initial fixation than the saccade target), perisaccadic percepts for upward saccades appeared similar to those for the other saccade directions (Fig. 2E; also see the nearer flash locations shown in Fig. 2A).

The above observations were also robust at the individual subject level. For example, Fig. 3, A and B, shows the same analyses as those made in Fig. 1, but for only one exemplary subject (male). For the same subject, the *top* row of Fig. 3, C and D, also replicates the analyses of Fig. 2. Thus all of the salient features of Figs. 1 and 2 can be seen in this example subject. The *middle* and *bottom* rows of Fig. 3, C and D, additionally show two more example subjects using the same formatting (with *subject c* being female). In both cases, similar observations to *subject a* were made. Finally, Fig. 3E shows the same summary analysis of Fig. 2B, but now for each of the remaining subjects in this experiment. In all seven subjects, upward saccades were always an outlier compared with horizontal and downward saccades when it came to perceptual mislocalization for flashes farther away from initial fixation than the saccade target. The fact that our results from the population data were replicated across individual subjects is also not too surprising because of the robustness and replicability of perisaccadic mislocalization in general (Ross et al. 1997).

We also confirmed that the outlying nature of upward saccades that we observed in Figs. 1–3 was not due to possible different time courses of mislocalization across different saccade directions. For example, it may have been the case that horizontal and downward saccades would exhibit as strong mislocalization as upward saccades but at different times from the 0- to 50-ms interval that we focused on in our analyses. However, this was not the case. For example, Fig. 4A plots full mislocalization time courses (along with 95% confidence intervals) for flashes farther from (*flash 1*) or nearer to (*flash 5*) initial fixation position than the saccade target. All saccade directions exhibited very similar times of peak perceptual mislocalization, with the difference being that upward saccades always had the strongest compression effect (e.g., compare the small black arrows in each of the panels in Fig. 4A). This was also true across individual subjects (Fig. 4B), and it was again also true for flashes that were additionally off the axis of the saccade vector (Fig. 4, C and D). Therefore, stronger perceptual mislocalization for upward saccades is not a result of our particular choice of analysis intervals in Figs. 1–3, and it is also a highly robust phenomenon that is readily evident at the individual subject level.

The results of Fig. 4 also confirm that upward saccades were indeed associated with perisaccadic changes in percept locations. Specifically, it may be argued that the longer term effect of Fig. 2, C and D, simply indicates that upward percepts are just biased. However, regardless of any potential biases (also

see Fig. 6B), upward saccades were indeed associated with a transient change in percept locations in perisaccadic intervals, exactly like other saccade directions.

Our next analysis was then concerned with whether variability in saccade metrics might account for differences in perisaccadic perceptual mislocalization for upward saccades. For example, saccade landing errors could be different for upward vs. downward saccades (Hafed and Chen 2016; Schlykowa et al. 1996; Zhou and King 2002). We thus performed control analyses in which we only included data for analysis that had identical variability of saccade end points (Fig. 5, A and B, see MATERIALS AND METHODS); in other words, there was maximal overlap in the distribution of saccade end points for all four saccade directions in these control analyses. We still replicated the findings of Figs. 1–3 (Fig. 5, C–H). This means that the stronger backward compression of farther flash locations for upward saccades was not an artifact of potential differences in saccade landing variability.

This similarity of results between the earlier analyses (e.g., Fig. 2) and those in which we restricted the range of saccade end points (Fig. 5) also suggests that the effects with upward saccades are distinct from potential impacts of saccade kinematics (for a given saccade size and direction) on the strength of perceptual mislocalization. For example, for a single saccade size and direction, variability in saccade kinematics can correlate with variability in mislocalization strength (Ostendorf et al. 2007), but this seems to be distinct from the phenomenon that we discovered in this study with upward saccades. To explore this idea even further, we repeated the analyses of Fig. 2B, but this time forcing a strict dissociation in saccade amplitudes across the different saccade directions. Specifically, for all of the rightward, leftward, and downward saccades, we only included data for analysis with saccade amplitudes greater than the median amplitude observed; then, for only upward saccades, we only included data with saccade amplitudes that were smaller than the median amplitude. These smaller saccades had smaller peak velocity, which should show weaker mislocalization strengths according to Ostendorf et al. (2007). Despite the smaller amplitudes, upward saccades were still associated with the strongest compression effect ($P = 1.58 \times 10^{-5}$, 1-way ANOVA). Therefore, the effects with upward saccades are distinct from those associated with potential correlations between saccade kinematics (for a single saccade direction and amplitude) and mislocalization strength.

Finally, our experimental design ruled out the possibility that mislocalization, and differences for upward saccades, were a result of a general bias to manually click near the center of the display, perhaps due to increased uncertainty (Brenner et al. 2008; Maij et al. 2010, 2011) about spatial and temporal reference frames perisaccadically (see MATERIALS AND METHODS). Therefore, stronger perisaccadic compression of farther flash locations for upward saccades was a robust observation.

Stronger orthogonal mislocalization for upward saccades, regardless of flash eccentricity relative to the saccade target eccentricity. The above-described results have focused on misperceptions parallel to the saccade vector. However, some of our flashes were also off the axis of the saccade (e.g., *flashes 2 and 4*). Previous studies have shown that such flashes are additionally mislocalized along a direction orthogonal to saccades (i.e., overall,
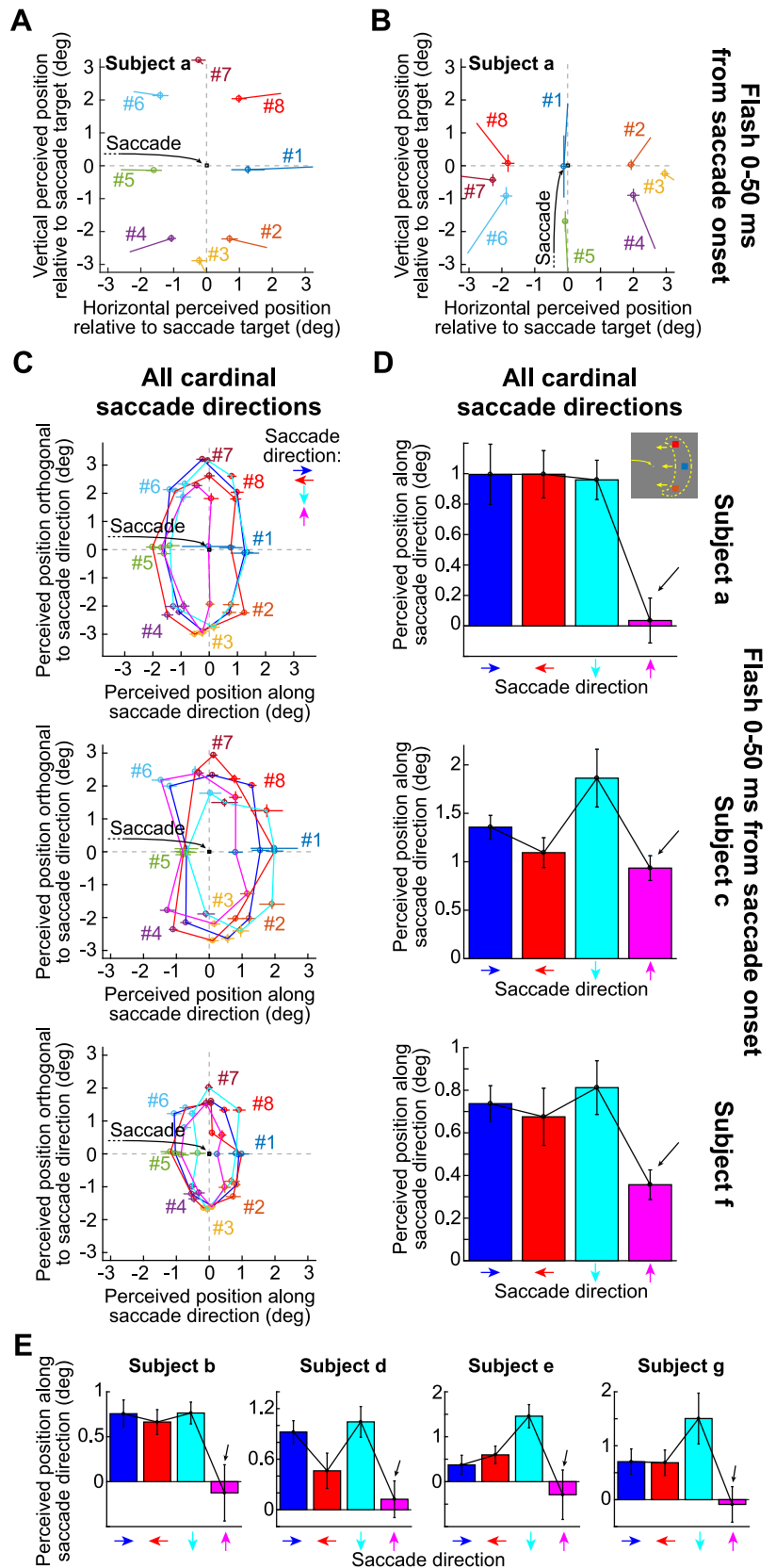
Fig. 3. Perisaccadic mislocalization patterns from individual subjects. The subjects exhibited the same patterns of results as those seen in the aggregate analyses of Figs. 1 and 2. *A*: same analysis as Fig. 1*A* for *subject a* ($n = 10–18$ trials per flash location for the time interval 0–50 ms from saccade onset, and $n = 11–19$ trials per flash location for the time interval 75–125 ms before saccade onset). *B*: same analysis as Fig. 1*B* for *subject a* ($n = 3–19$ trials per flash location for 0–50 ms from saccade onset, and $n = 11–21$ for 75–125 ms before saccade onset). *C* and *D*: each row shows results from a sample subject, using formatting identical to that in Fig. 2, *A* and *B*. *Top* row shows data from the same subject as in *A* and *B*. For this subject, $n = 113, 125, 125,$ and 101 saccades for rightward, leftward, downward, and upward saccades, respectively. For the same subject in *D*, *top row*, $P = 1.252 \times 10^{-4}$, 1-way ANOVA; *inset* shows schematic. *Middle* and *bottom* rows highlight 2 additional subjects with similar conclusions. *Subject c* (*middle* row) was female. *E*: summary analyses as in Fig. 2*B* but for all 4 remaining individual subjects recruited in this experiment. In all cases, the clear outlying nature of upward saccades was obvious (small black arrows).
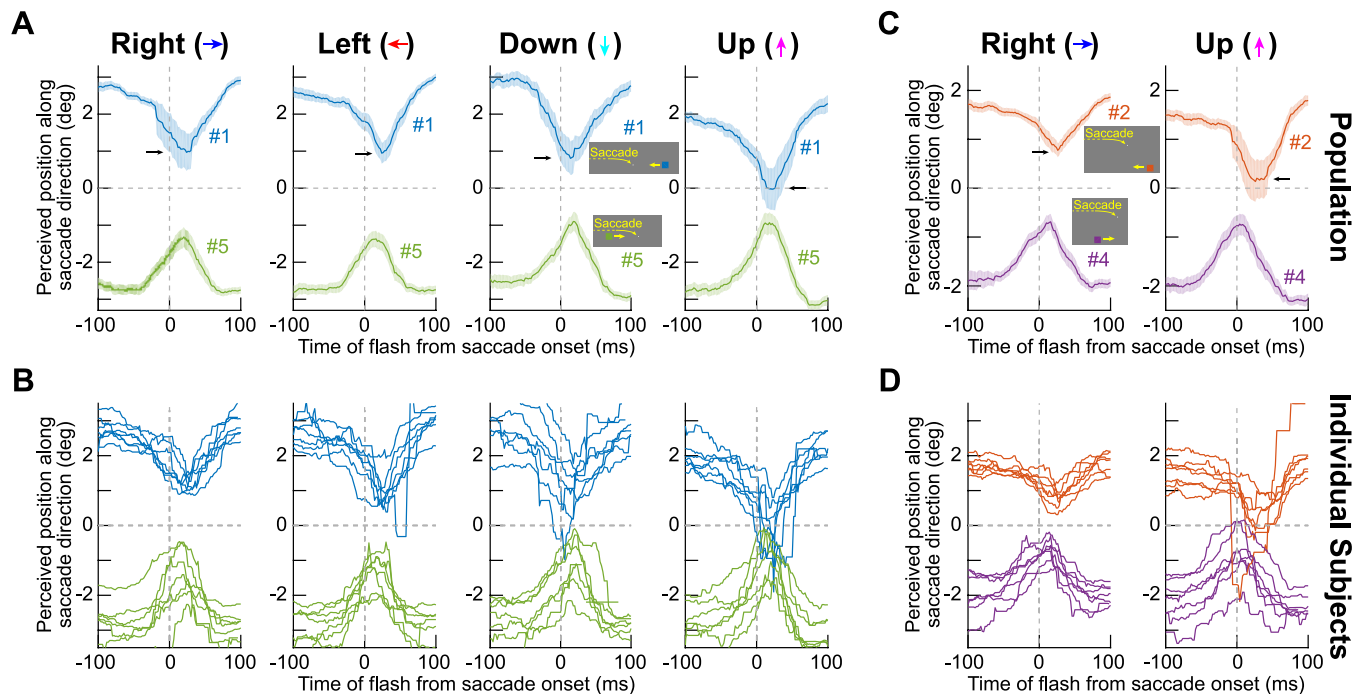
Fig. 4. Time courses of perisaccadic perceptual mislocalization for different saccade directions. *A*: each panel shows perceived flash position (relative to saccade target location) along the direction of the saccade vector for either a flash farther away from initial fixation than the saccade target (*flash 1*) or a flash nearer to initial fixation than the saccade target (*flash 5*). Error bars (shading) denote 95% confidence intervals, and each panel shows results for a given saccade direction. Mislocalization time courses were similar across saccade directions, but the strength of mislocalization (e.g., horizontal black arrows) was always highest for upward saccades. Thus the results in Figs. 1–3 were not due to our particular choice of analysis windows (0–50 ms from saccade onset). Each shown time bin had *n* = 60–130 repetitions. *B*: the same analyses as in *A* but for each individual subject, supporting conclusions similar to those made in Figs. 1–3 and *A*. *C* and *D*: same analyses as in *A* and *B*, respectively, but repeated for example off-axis flash locations. For simplicity, only rightward and upward saccades are shown, but the same conclusions as in *A* and *B* were made even for these off-axis flash locations, and even when all 4 saccade directions were analyzed. *Insets* show schematics.

there is oblique perceptual mislocalization) (Kaiser and Lappe 2004). Moreover, whether a flash is farther from (e.g., *flash 2*) or nearer (e.g., *flash 4*) to the saccade target dictates an asymmetry in orthogonal mislocalization (Kaiser and Lappe 2004), which current models account for by the fact that nearer eccentricities are magnified in neural tissue compared with farther eccentricities (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010).

Consider, for example, the scenario shown in Fig. 6*A*, *top*, for rightward saccades. Both *flashes 2* and *4* would be expected to experience orthogonal mislocalization. However, orthogonal mislocalization is expected to be stronger for *flash 2* than for *flash 4* (Kaiser and Lappe 2004) such that if one were to draw a mislocalization "vector" (with origin being the percept long before or after a saccade and end being the percept perisaccadically), then such a vector would be more oblique for *flash 2* than for *flash 4* (Fig. 6*A*, *top*). We replicated this finding (Kaiser and Lappe 2004) for rightward saccades (Fig. 6*A*, *bottom*, saturated colors); we plotted the trajectory of perceived flash position from −100 to +100 ms relative to saccade onset and in steps of 2 ms (see MATERIALS AND METHODS). We then monitored the orthogonal component of the percept trajectory. As can be seen from the saturated colors in Fig. 6*A*, *bottom*, the mislocalization trajectory was indeed more oblique for *flash 2* than for *flash 4* (i.e., the orthogonal component of mislocalization was stronger), even though the flashes were otherwise symmetric with respect to the saccade target (Kaiser and Lappe 2004). However, repeating the same analysis for upward saccades revealed a different pattern: orthogonal mislocalization

was as strong for *flash 4* as it was for *flash 2* (Fig. 6*A*, *bottom*, unsaturated colors). In other words, for upward saccades, there was strong orthogonal mislocalization even for flashes nearer to initial fixation than the saccade target, unlike in Kaiser and Lappe (2004) and unlike for the rightward saccade (shown with the saturated colors in the same figure).

This observation was also evident when we plotted time courses of perisaccadic perceptual mislocalization for *flashes 2* and *4*. In each column of Fig. 6*B*, the *top* panel illustrates perceived position (along with 95% confidence intervals) of either *flash 2* or *flash 4* along the dimension parallel to the saccade vector (see MATERIALS AND METHODS; also similar to Fig. 4), whereas the *bottom* panel illustrates perceived position (along with 95% confidence intervals) of the same flashes orthogonal to the saccade. Because the two flashes were either more or less eccentric than the saccade target, parallel perceived positions were expected to become compressed toward the saccade target (i.e., to move closer to 0 in the *top* row) regardless of saccade direction. This was indeed the case (e.g., 0–50 ms from saccade onset; shaded gray bars in Fig. 6*B*). However, if neural maps responsible for perisaccadic mislocalization were purely symmetric (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010), then the orthogonal component of perceived position (Fig. 6*B*, *bottom*) should have revealed a strong asymmetry (Kaiser and Lappe 2004) like that predicted by Fig. 6*A*, *top*, for all saccade directions. This was violated for upward saccades (Fig. 6*B*, *bottom* row and diagonal black arrow in the rightmost panel); in the period of maximum
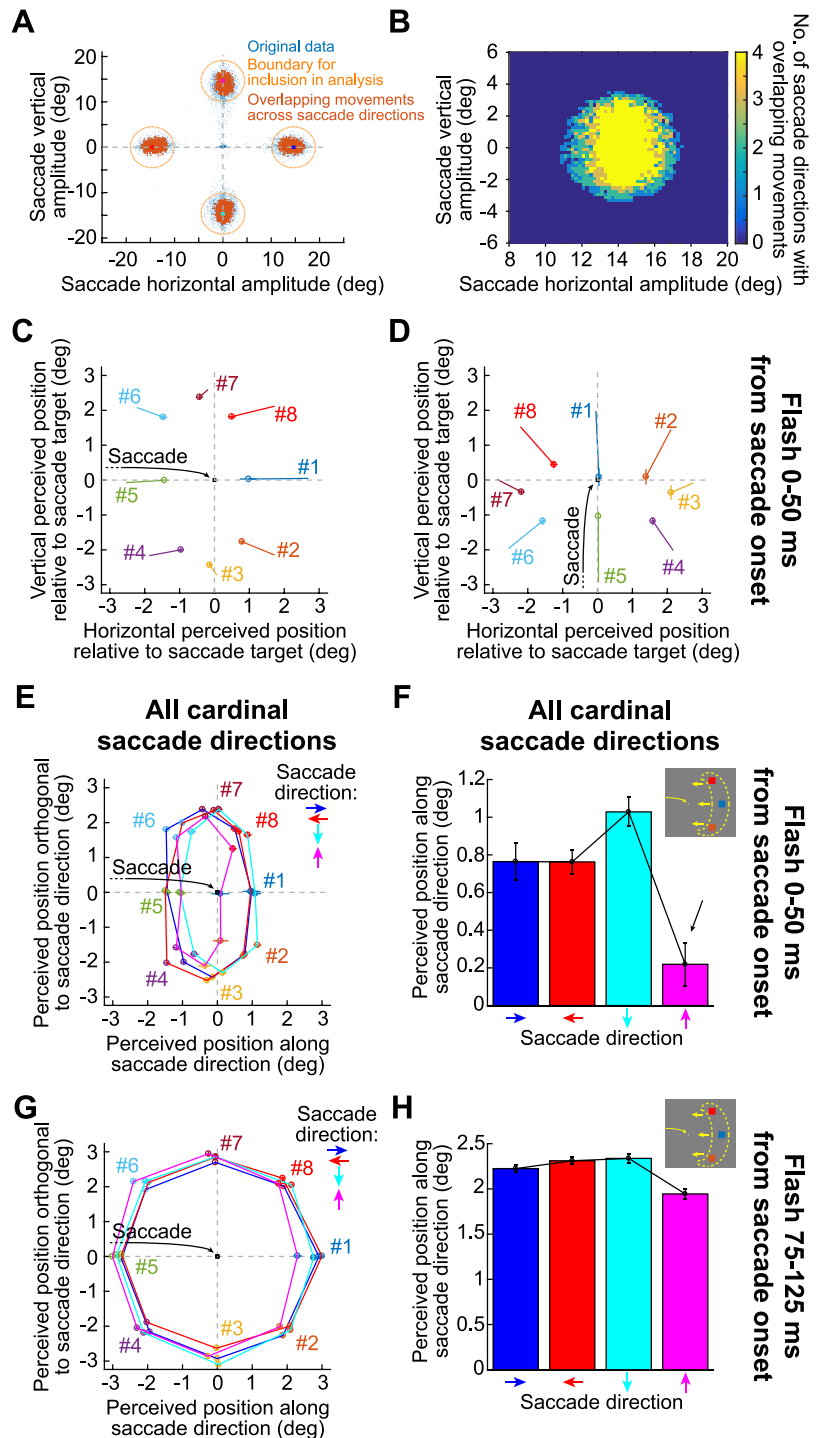
Fig. 5. Controlling for variability of saccade end points. *A*: each blue dot shows the horizontal and vertical amplitude of a saccade; colored squares show the saccade target positions. Only trials in which saccades landed within the dashed orange circle for each saccade direction were analyzed, to ensure that subjects made a proper saccade when instructed to do so. Saccadic and/or manual reaction time outliers were excluded in all analyses (see MATERIALS AND METHODS). In additional control analyses, only trials in which saccade amplitudes and directions had overlap across all analyzed trials among the 4 saccade directions in this experiment (brown dots) were analyzed. In other words, if all the brown dots were rotated to align with a rightward saccade direction, then all 4 saccade directions would have matched variability in saccadic end points. *B*: the regions of overlap in *A* were established by rotating all saccade directions and plotting a cumulative histogram of saccade landing positions. The yellow region shows that this region was covered by all 4 saccade directions, and it was used to pick only the overlapping saccades of *A*. Similar overlap criteria were also used to perform control analyses in the second experiment involving diagonal saccades. *C* and *D*: same analyses as in Fig. 1, *A* and *B*, but with only overlapping saccades. Stronger compression of flashes farther away from the saccade target relative to initial fixation in upward saccades still occurred. *E* and *F*: same analyses as in Fig. 2, *A* and *B*, again showing that the results associated with upward saccades did not depend on potential differences in variability of saccadic landing positions across different saccade directions. For *F*, $P = 1.95 \times 10^{-8}$, 1-way ANOVA. *G* and *H*: similar analyses at a different time point, again replicating the results of Fig. 2. *Insets* show schematics.

mislocalization (shaded gray bars), orthogonal percepts were similar for *flashes 2* and *4* with upward saccades, but not for the other saccade directions.

We next summarized these orthogonal mislocalization results, but for all off-axis flash locations that also had a nearer or farther eccentricity component relative to the saccade target (i.e., *flashes 2, 4, 6,* and *8*). In Fig. 7*A*, we plotted the orthogonal component of perceived flash location for nearer off-axis flashes (i.e., *flashes 4* and *6*), and in Fig. 7*B*, we plotted the same variable for farther off-axis flashes (i.e., *flashes 2* and *8*). In both cases, orthogonal mislocalization clearly depended on saccade direction ($P =$

7.61×10^{-11}, 1-way ANOVA for Fig. 7*A*, and $P = 1.72 \times 10^{-10}$, 1-way ANOVA for Fig. 7*B*). Importantly, orthogonal mislocalization was always the strongest for upward saccades (i.e., the percept was closest to 0 in the figure; this is also evident in Figs. 2*A* and 3*C*). Therefore, upward saccades were not only associated with stronger parallel compression of farther flash locations (Figs. 1–5), but they were also associated with stronger orthogonal mislocalization even for nearer flash locations (Figs. 6 and 7). Note also that in Fig. 7*B*, percepts were generally more mislocalized (i.e., closer to 0 on the *y*-axis) than in Fig. 7*A*, confirming that orthogonal mislocalization is stronger for farther
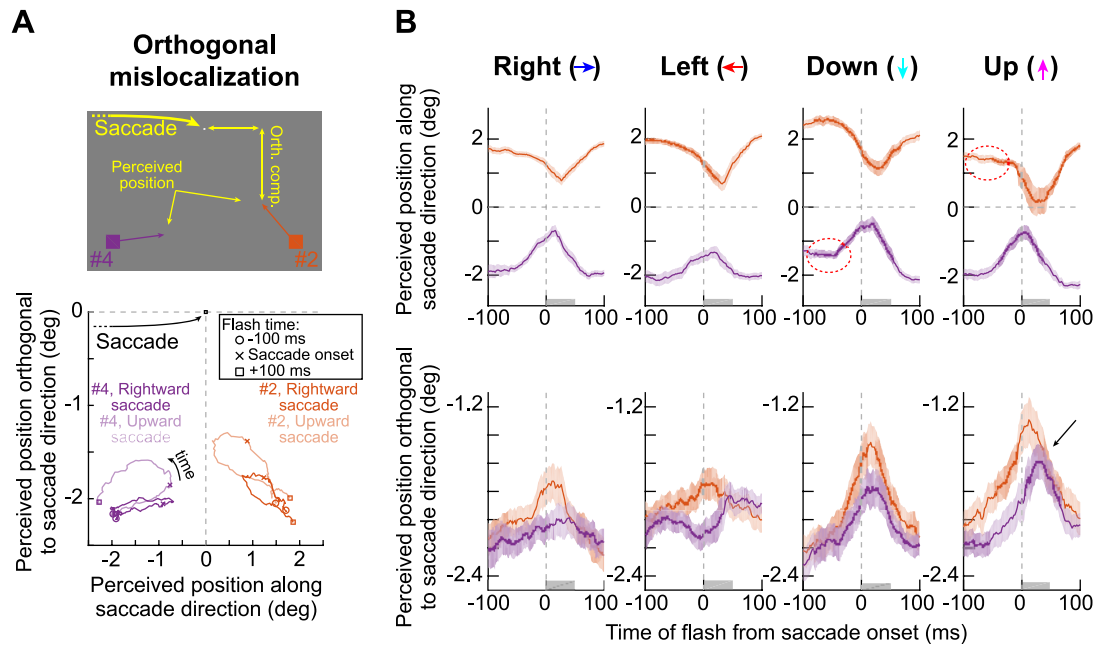
Fig. 6. Mislocalization orthogonal to saccade direction was strongest for upward saccades, even for flash locations nearer to initial fixation than the saccade target. *A*: it was previously shown that mislocalization orthogonal to saccade direction is asymmetric for flashes nearer or farther away from the saccade target. For example, the schematic (*top*) shows a rightward saccade and *flashes 2* and *4*. The orthogonal perceived position of *flash 2* (Orth. comp.) should be closer to the saccade target than that of *flash 4*, resulting in "mislocalization vectors" having different slopes (orange and purple arrows). The graph (*bottom*) plots the trajectory of perceived position for these 2 flash locations from −100 to +100 ms relative to saccade onset, and this was done for either rightward or upward saccades (rotated as in Figs. 2–4 to facilitate comparison with rightward saccades). For rightward saccades (saturated colors), the difference in mislocalization trajectory slopes was confirmed: the mislocalization vector for *flash 4* had shallower slope than that for *flash 2*. For upward saccades (unsaturated colors), orthogonal mislocalization was strong even for nearer flash locations (compare the mislocalization vector slopes). In *A*, n = 417 and 411 trials for *flashes 2* and *4*, respectively, for the rightward saccade; n = 372 and 396 trials for the same flash locations for the upward saccade. *B*: time courses of perceived flash position (relative to saccade target location) as a function of time from saccade onset for different saccade directions (columns). *Top* row shows perceived position along saccade direction (error bars are 95% confidence intervals) demonstrating expected compression (also see Fig. 4). *Bottom* row shows the component of perceived position orthogonal to saccade direction. For all but the upward saccade, during the interval 0–50 ms (shaded gray bars), orthogonal mislocalization was stronger (i.e., closer to zero y-axis values) for farther (*flash 2*, orange) than nearer (*flash 4*, purple) flashes. Upward saccades violated this observation (black arrow). Also note that both upward and downward saccades generally had much stronger orthogonal mislocalization than horizontal saccades (*bottom* row). Each time bin shown had n = 60–238 repetitions. Dashed red ellipses depict bias percepts in the parallel component of flash location before saccade onset for a downward saccade (*flash 4*) and an upward saccade (*flash 2*), as discussed in detail in the text.

rather than nearer flash locations relative to the saccade target location (Kaiser and Lappe 2004).

As in the case of our parallel mislocalization results, we also checked that these orthogonal mislocalization observations were robust at the individual subject level. This was the case. For example, for all farther flash locations, for which strong orthogonal mislocalization is the most expected (Kaiser and Lappe 2004), all of our subjects showed the strongest mislocalization when upward saccades were executed (Fig. 7D); *subject c* also showed equally strong orthogonal mislocalization for downward saccades (but not horizontal ones). For nearer flash locations, for which weaker orthogonal mislocalization might be expected (Kaiser and Lappe 2004), all subjects (except *subject e*) still showed strong orthogonal mislocalization for upward saccades (and to a lesser extent also downward saccades) compared with other saccade directions (Fig. 7C). Thus the results from Fig. 6 and Fig. 7, A and B, were robust at the individual subject level.

We were also intrigued by several other details evident in the time courses of Fig. 6B. For example, for upward saccades, there was a biased percept in the parallel component of flash location for *flash 2* long before saccade onset (Fig. 6B, *top* row, upward saccade, dashed red ellipse). This bias means that subjects reported *flash 2* as being lower than it really was even 100 ms before saccade onset (well before the perisaccadic

transient deflection in percept started to occur). However, this does not necessarily mean that subjects had an overall bias to click slightly more downward only for upward saccades (or only for locations in the upper visual field relative to the head), and it also does not mean that our results described above (Figs. 1–7) are fully explained by simple click biases associated with upward saccades. Specifically, the same early bias in percept well before saccade onset was also evident for downward saccades (i.e., with locations in the lower visual field relative to the head), but this time in association with *flash 4* (Fig. 6B, *top* row, downward saccade, dashed red ellipse). In this case, subjects perceived this flash location as being more downward than it really was even 100 ms before saccade onset, and once again, well before the perisaccadic transient distortion in perception began to emerge. Interestingly, in both of these cases, *flash 2* for upward saccades and *flash 4* for downward saccades were in reality physically above the saccade target location. This means that in addition to perisaccadic mislocalization being directly tied to saccade vectors (Kaiser and Lappe 2004; Ross et al. 1997), additional factors related to flash location itself (e.g., being physically up) matter. What is it, then, about retinotopic flash location that can influence percepts in our task? Related to this, why was the orthogonal percept in Fig. 6B, *bottom*, apparently so different in nature between rightward and leftward saccades (e.g., weaker mislo-

calization bump in the curve for *flash 2* and different temporal pattern in the curve for *flash 4*), even though both were horizontal eye movements? We next turn to exploring these additional intriguing questions.

Different mislocalization patterns of upper vs. lower visual field flash locations for horizontal saccades. Even though our analyses of Fig. 7 summarized all off-axis flash locations having nearer or farther components (*flashes 2*, *4*, *6*, and *8*),
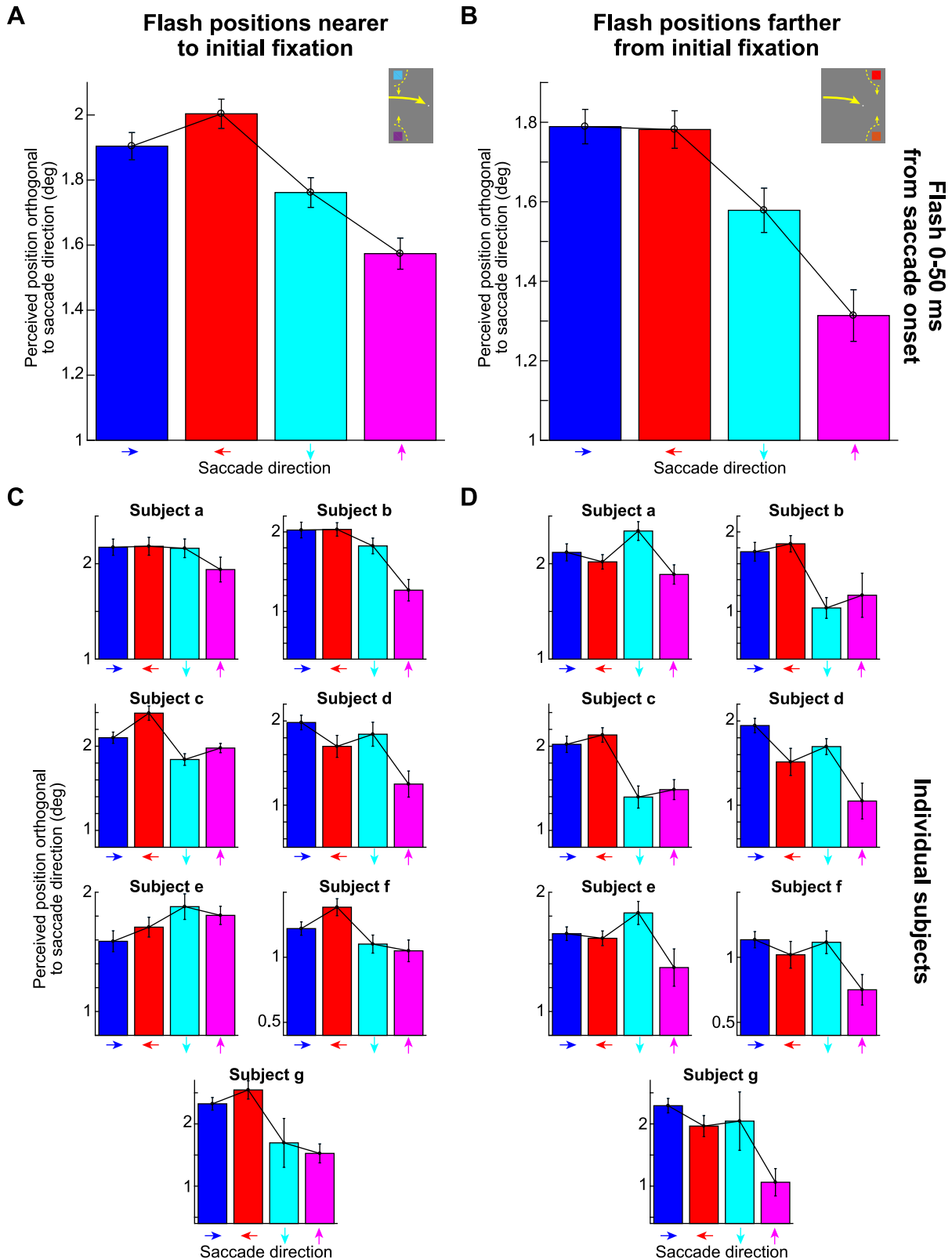
Fig. 6*B* only showed time courses of mislocalization for *flashes 2* and *4*. In Fig. 6*B*, orthogonal mislocalization seemed to be conspicuously almost absent for the leftward saccade, and even for the *flash 2* location (Fig. 6*B*, *bottom*, leftward saccade). This is very different from rightward saccades (Fig. 6*A*, saturated colors) (Kaiser and Lappe 2004). We explored this apparent discrepancy by comparing retinotopic flash locations in more detail. Specifically, because of our convention to relate flash eccentricity to saccade target eccentricity (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010) independently of saccade direction, and because we rotated data to a single reference frame (Figs. 2–7), *flashes 2* and *4* for the leftward saccade were in reality in the upper visual field retinotopically, whereas they were in the lower visual field for rightward saccades. Therefore, we replotted perisaccadic percept trajectories associated with rightward and leftward saccades (similar to Fig. 6*A*), but this time maintaining the original raw coordinates (Fig. 8, *A* and *B*). We found that orthogonal mislocalization for off-axis flashes with nearer and farther components (i.e., *flashes 2, 4, 6,* and *8*) was much weaker for upper visual field flashes than for lower visual field ones, independently of whether a saccade was rightward or leftward (Fig. 8, *A* and *B*). Lower visual field flashes showed results consistent with Kaiser and Lappe (2004) in the sense that farther flashes had stronger orthogonal perisaccadic mislocalization than nearer ones (Fig. 8, *A–F*). Thus, for horizontal saccades, orthogonal perceptual mislocalization was replicated (Kaiser and Lappe 2004), but only for lower visual field flash locations. These results are intriguing because they indicate that not only saccade vector direction matters for perisaccadic perceptual mislocalization patterns (Figs. 1–7); retinotopic flash location also does matter (Fig. 8). Interestingly, closer inspection of the results of Kaiser and Lappe (2004) with rightward saccades does indeed show that orthogonal mislocalization in their data was also weaker for upper visual field flashes than for lower visual field flashes, consistent with our results.

Interaction between saccade direction vector and flash location for diagonal saccades. To further demonstrate that both saccade direction and flash location matter, we ran six subjects on a second experiment involving diagonal saccades (~14.6° amplitude in the 45° rightward upward or rightward downward direction; see MATERIALS AND METHODS). Figure 9, *A* and *B*, shows the results of mislocalization in the same format as in Fig. 1. Two-dimensional perisaccadic mislocalization was always aligned to the saccade vector (i.e., there was, in general, compression toward the saccade target along the saccade vector), and this is consistent with accounts of mislocalization relying on flash eccentricity relative to saccade target eccentricity (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010).

However, there were still differences in mislocalization as a function of saccade direction. For example, in Fig. 9*C*, we directly superimposed perisaccadic percepts for diagonal upward and diagonal downward saccades using the same coordinate transformation (e.g., Fig. 2*A*). If neural maps responsible for perisaccadic perceptual mislocalization were perfectly directionally symmetric (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010), then the two contours shown in Fig. 9*C* should overlap. However, there are clear distortions, with diagonal upward saccades showing stronger mislocalization (also see Fig. 9*D*), especially for upper visual field flash locations (e.g., *flashes 6* and *7*; Supplementary Video S1). Interestingly, for some flashes, diagonal saccades were associated with as strong mislocalization as with purely upward saccades in the first experiment (Fig. 9, *E* and *F*). Also, as in our first experiment, these differences between diagonal upward and diagonal downward saccades were evident even on the individual subject level (Fig. 10). Finally, when we plotted time courses of perceived flash positions for different flash locations in diagonal saccades, we found that the strongest mislocalizations (in the 0- to 50-ms perisaccadic intervals) tended to occur when both the saccade direction and flash location had an upward component to them (Fig. 11). Thus asymmetries in perceptual mislocalization for upward saccades compared with other cardinal directions also extended to cases with oblique saccades, as well.

Implications for neural circuits involved in perisaccadic mislocalization. In all, our results do not contradict the idea that foveal magnification plays a role in perisaccadic perceptual mislocalization (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010). However, these same results also suggest that the directional symmetry inherent in such accounts may be overly simplistic. To demonstrate this, we asked whether a simple neural circuit principle could make our results plausible. Our goal was not to exhaustively model and/or fit data, but rather to test the conceptual plausibility of the hypothesis that tissue asymmetries beyond foveal magnification can give rise to differential patterns of perisaccadic mislocalization (also see DISCUSSION). Our starting point was a common agreement among models (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010) that neural maps with foveal magnification can account for mislocalization. Although we are ambivalent to the details of individual models, we picked the simplest instantiation of them (VanRullen 2004), in which read-out of flash location is done after a simple translation of neural activity from the periphery (where the flash is presented) to the fovea (where the read-out of flash location takes place postsaccadically) (VanRullen 2004).

Fig. 7. Orthogonal mislocalization relative to saccade direction was strong for upward saccades even for near flash locations. *A*: for all flash locations nearer to initial fixation than the saccade target, and that could still experience orthogonal mislocalization relative to saccade direction (i.e., *flashes 4* and *6*), the average perceived position of the flash orthogonal to the axis of a saccade vector was plotted for flashes 0–50 ms from saccade onset. As in all analyses, perceived position was calculated relative to the saccade target location, meaning that smaller values in the plot indicate stronger compression. Consistent with Fig. 6, the upward saccade had the strongest orthogonal mislocalization even though the flashes analyzed were nearer to initial fixation than the saccade target. *B*: this effect was magnified even more for all flashes farther away from the saccade target (i.e., *flashes 2* and *8*). Thus orthogonal mislocalization was prominent for upward saccades, even for flashes nearer to initial fixation than the saccade target. Note that the *y*-axes are different in *A* and *B*, and they confirm that orthogonal mislocalization for horizontal saccades is stronger for farther than nearer flash locations. Error bars denote SE (n = 166, 164, 165, and 178 trials for rightward, leftward, downward, and upward saccades in *A*, respectively, and n = 173, 172, 189, and 156 trials for rightward, leftward, downward, and upward saccades in *B*). *Insets* show schematics. *C* and *D*: same analyses as in *A* and *B*, respectively, but for each individual subject.

Fig. 8. For horizontal saccades, mislocalization patterns differed between flashes in the upper vs. lower retinotopic visual fields. *A* and *B*: a closer look at the phenomenon of orthogonal mislocalization from Figs. 6 and 7. For leftward (*A*) or rightward (*B*) saccades, mislocalization trajectories were plotted (similar to Fig. 6*A*) for all flash locations that were either farther (*flashes 2* and *8*) or nearer (*flashes 4* and *6*) from initial fixation than the saccade target and that could still experience orthogonal mislocalization. Each curve plots the percept trajectory for a given flash location from −100 to +100 ms from saccade onset, and the arrow connects the baseline percept (midpoint of −100-ms and +100-ms percepts) to the point in each percept trajectory with maximal horizontal mislocalization. Independently of saccade direction, flashes in the lower visual field (*flashes 6* and *8* for leftward saccades and *flashes 4* and *6* for rightward saccades) had asymmetric orthogonal mislocalization (differences in mislocalization vector slopes between nearer and farther flash locations), as shown for the rightward saccade in Fig. 6 and also as shown previously (Kaiser and Lappe 2004). However, flashes in the upper visual field only experienced parallel mislocalization with no orthogonal component (mostly horizontal mislocalization vectors). *C* and *D*: this observation was confirmed when the time courses of vertical perceived position of the upper visual field flashes were plotted. There was no strong perisaccadic modulation in vertical perceived position. *E* and *F*: however, for flashes in the lower visual field, vertical perceived position changed perisaccadically, and the mislocalization patterns also confirmed previous observations that farther flash locations (*flash 8* for leftward saccades and *flash 2* for rightward saccades) experienced stronger orthogonal mislocalization than nearer flash locations (*flash 6* for leftward saccades and *flash 4* for rightward saccades) (Kaiser and Lappe 2004). Thus retinotopic upper or lower visual field flash location is a contributor to differences in percepts for different saccade directions. Error bars denote 95% confidence intervals, and each time bin included 75–132 repetitions. *Insets* show schematics.
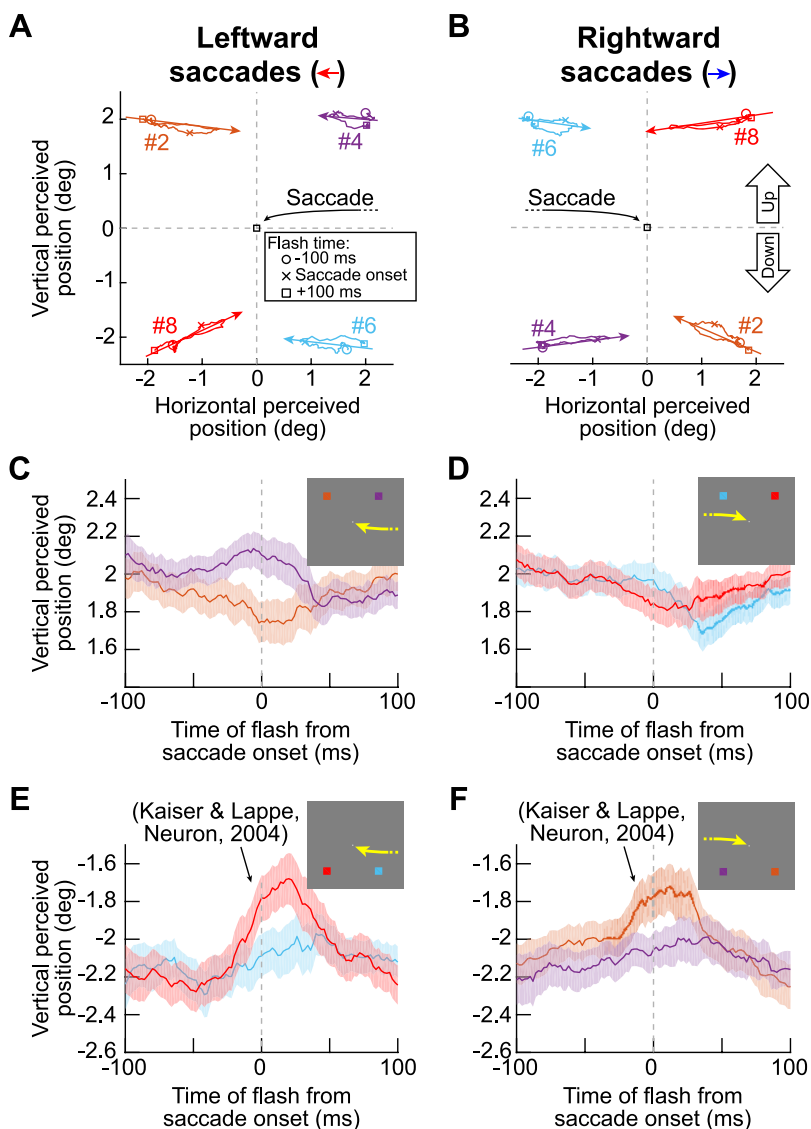
In the map of Fig. 12*A* (see MATERIALS AND METHODS), if there was a flash around an upward saccade target, then the flash would be around the magenta square (e.g., 1 of the 5 shown flash locations). The saccade would translate this neural activity to the fovea (along the trajectory shown by the magenta arrow). The resulting percept would emerge by reading out the translated flash locations, which are shown by the magenta contour in the foveal representation of Fig. 12*A* (i.e., after the saccade). In Fig. 12*A*, we implemented such an idea on a map exhibiting not only foveal magnification (VanRullen 2004) but also an asymmetry between the representations of the upper and lower visual fields (Hafed and Chen 2016) (see MATERIALS AND METHODS). We also repeated the same exercise for horizontal (blue arrow) and downward (cyan arrow) saccades. Using this particular example map, based on physiological results from the SC (Hafed and Chen 2016), upward saccades (magenta arrow and contours in the foveal representation of Fig. 12*A*) would indeed result in foveal neural activity of flash locations (i.e., for read-out of the percept) that is an outlier compared with all other cardinal saccade directions (other contours in the foveal region of the map in Fig. 12*A*). With a purely symmetric neural map exhibiting only foveal magnifi-

cation (Fig. 12*B*), as in the scheme of VanRullen (2004) and related models, none of the saccade directions would be outliers. Of course, this does not necessarily address the question of how maps are actually read out, but it nonetheless demonstrates that when two-dimensional representations and foveal magnification are considered, there are radial-tangential asymmetries in visual representations that have the potential to result in upward saccades looking like outliers in the data (as we saw experimentally).

Interestingly, a map such as that in Fig. 12*A* would also predict an asymmetry between upper and lower visual field flash locations even for purely horizontal saccades (e.g., Fig. 8) because of the asymmetry in the map itself. It is also interesting to note that when a visual transient in the retina and beyond is caused by a stimulus onset rather than a saccade, mislocalizations can still occur (Zimmermann et al. 2014a), suggesting that perisaccadic mislocalization has a strong visual component (Zimmermann et al. 2014b). Because maps like the SC are visually sensitive, and with spatial and temporal neural dynamics conceptually similar to those in purely visual areas (Chen and Hafed 2018), it is conceivable that the same mechanism
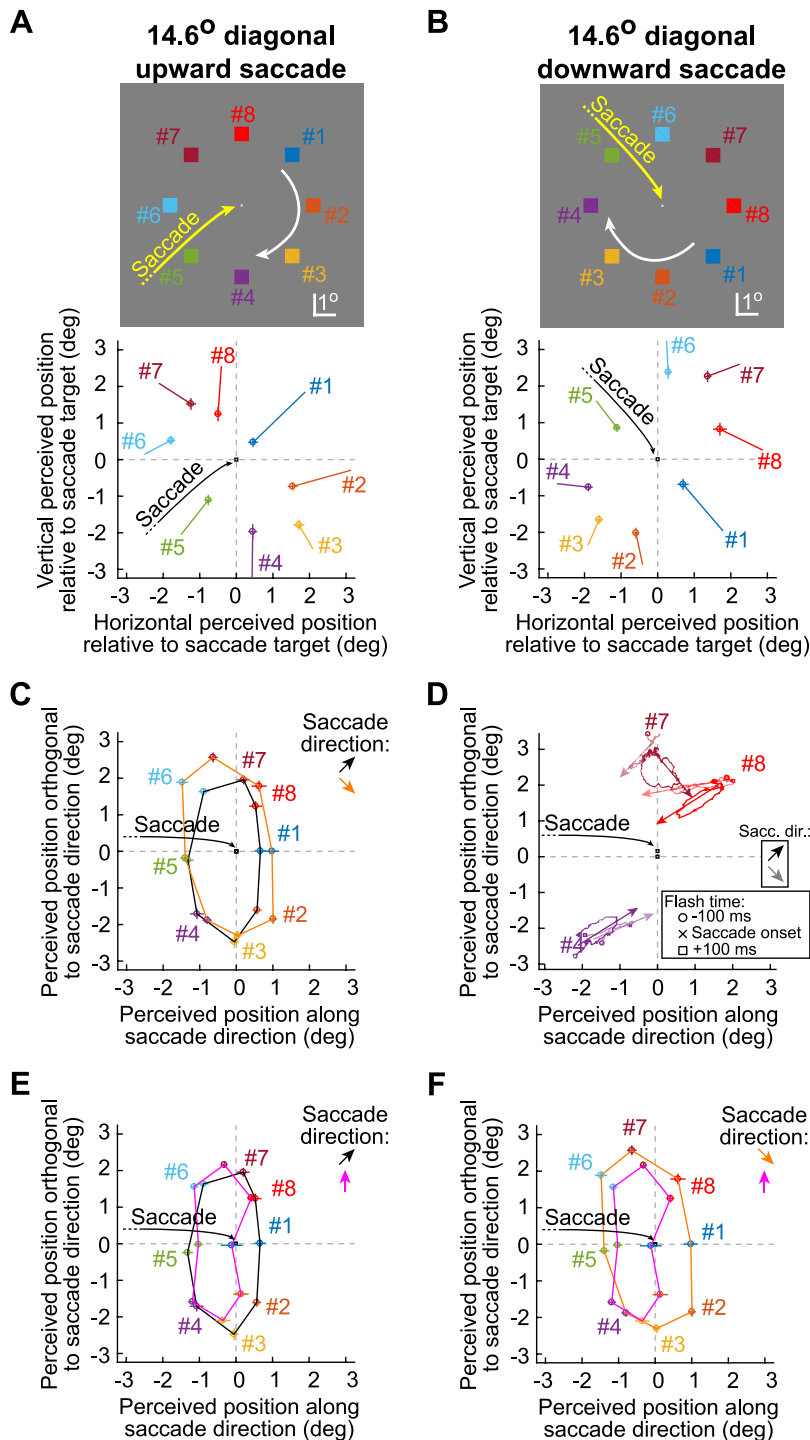
Fig. 9. Diagonal saccades revealed mislocalization asymmetries beyond classic compression based on flashes being farther or nearer from the saccade target relative to initial fixation. *A* and *B*: perceived flash position is plotted (for flashes occurring 0–50 ms from saccade onset) for either diagonal upward (*A*) or diagonal downward (*B*) saccades. Schematics (*top*) show identical flash locations relative to the saccade target as in our earlier experiment, and with similar conventions relative to saccade target location and saccade direction. Graphs (*bottom*) show percept locations, along with error bars denoting SE. The origin of the line connected to each individual data point illustrates the location of the percept when the corresponding flash occurred 75–125 ms before saccade onset (as in Fig. 1). Both diagonal saccades were associated with compression toward the saccade target, but there were notable differences in the patterns of compression. *C*: both saccades were rotated to the standard reference frame to demonstrate the differences in compression between diagonal upward and diagonal downward saccades. Diagonal upward saccades showed substantially stronger compression for flash locations (i.e., *flashes 7* and *8*) that were located physically higher in the display relative to the saccade target than for diagonal downward saccades. Figure 10 shows the same analyses but using data from individual subjects to demonstrate robustness of the phenomenon even on the individual subject level. *D*: percept trajectories (as in Figs. 6 and 8) for example flash locations demonstrating similarities (*flash 4*) or differences (*flashes 7* and *8*) between the diagonal upward (saturated colors) and diagonal downward (unsaturated colors) saccades. Data in *D* are formatted identically to a similar analysis in Fig. 8. Supplementary Video S1 shows an animation of these trajectories from 2 sample subjects (those highlighted in Fig. 10, *A–F*). For *A–C*, *n* = 520 and 583 trials for diagonal upward and diagonal downward saccades, respectively, in the interval 0–50 ms from saccade onset; also, each time bin in the trajectories of *D* had 57–116 repetitions. *E*: data from the diagonal upward saccade (black) plotted along with those from a purely upward saccade (magenta) for comparison. Diagonal upward saccades were associated with similar distortions in percepts for flashes nearer to initial fixation than the saccade target. *F*: same comparison as for upward saccades but for the diagonal downward saccades (orange). Diagonal downward saccades were associated with different patterns of percepts than the diagonal upward saccades. Thus patterns of perisaccadic mislocalization depend on saccade direction.

above can account for visual-only mislocalizations in the absence of saccades.

Similarly, when the same translation mechanism is simulated on the asymmetric map for diagonal saccades (Fig. 12*C*), then percepts associated with diagonal upward vs. diagonal downward saccades would be distorted with respect to each other, just like in our data (Figs. 9–11). This would again not be the case with a purely symmetric map (Fig. 12*D*). Thus an asymmetry beyond foveal magnification in neural maps is a plausible mechanism for our observation that perisaccadic perceptual mislocalization is different for upward saccades.

DISCUSSION

We observed a difference in perisaccadic perceptual mislocalization for upward saccades compared with other cardinal saccade directions. We also noticed that even for purely horizontal saccades, upper vs. lower visual field retinotopic flash locations experience different patterns of perisaccadic perceptual mislocalization. We think that these results are particularly interesting because they touch on a broader question of how different sensory, sensory-motor, and motor maps in the brain interact around the time of saccades in order to ensure trans-
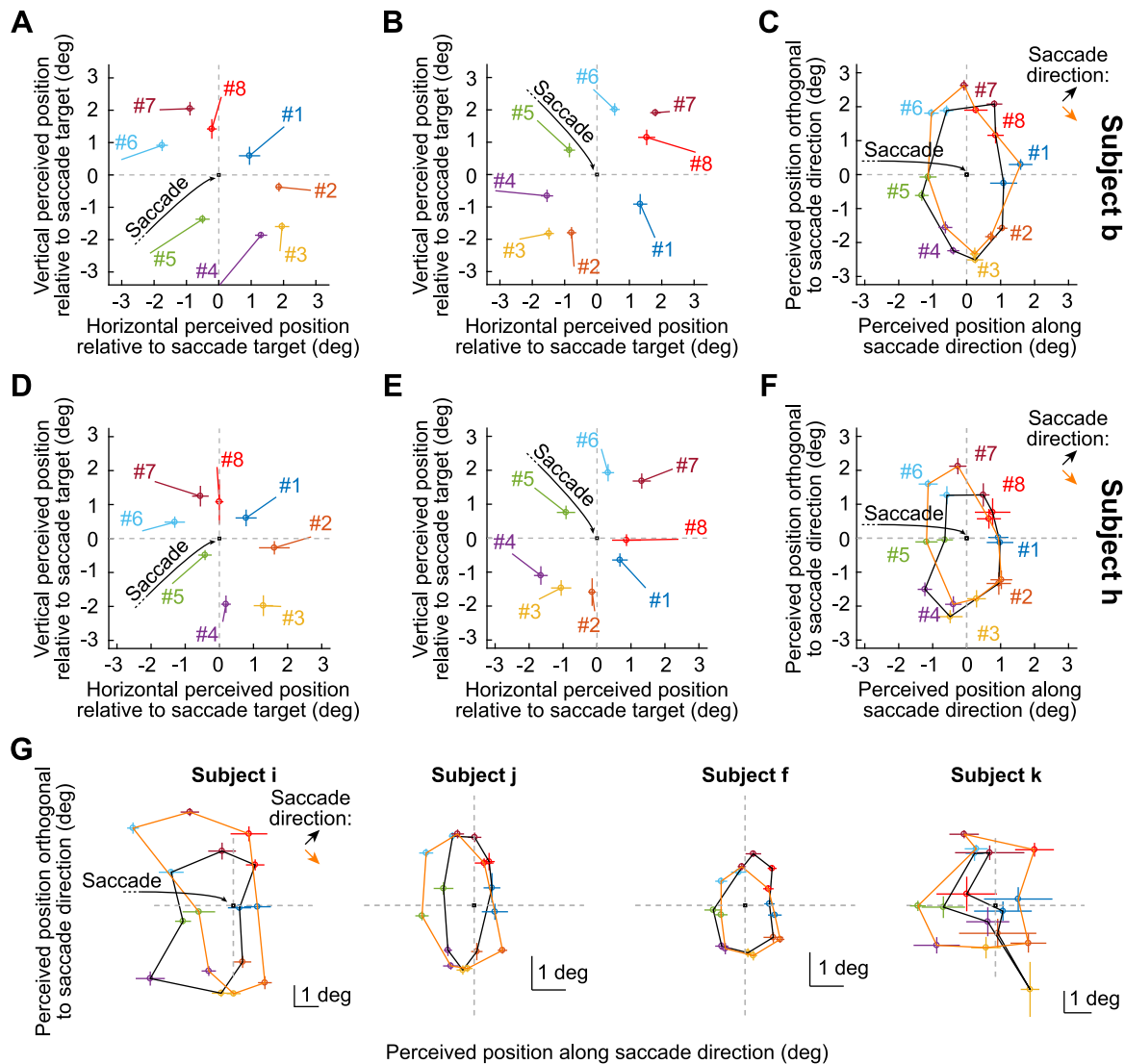
Fig. 10. Perisaccadic mislocalization for diagonal saccades in individual subjects. *A–C*: analyses are identical to those shown in Fig. 9, *A–C*, but using data from only a single subject (female). The same differences between diagonal upward and diagonal downward saccades were evident even on an individual subject basis. Error bars denote SE. *D–F*: similar results from a second example subject. Supplementary Video S1 shows time courses of percept trajectories for the data from these 2 subjects (*subjects b* and *h*) combined. *G*: all remaining 4 subjects showed asymmetries in perceptual mislocalization across diagonal upward and diagonal downward saccades. In all cases, the black and orange lines did not overlap with each other.

saccadic perceptual stability. Specifically, if perisaccadic perceptual mislocalization really does depend on neural tissue distortions (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010), then a significant question is, what happens if some neural maps involved in the phenomenon have additional asymmetries (beyond foveal magnification) that are not present in other maps functionally connected to them at the time of saccades? For example, if the SC has upper visual field magnification (Hafed and Chen 2016), whereas the primary visual cortex (V1) or area V4 does not, then how might these different neural maps interact with each other during perisaccadic intervals if the maps were critical for creating the perceptual phenomenon? Similarly, if some areas have upper/lower visual field asymmetries and others do not, then perhaps observations like ours can pinpoint potential neural loci for perisaccadic perceptual mislocalization.

Such loci are not necessarily known, and there is an urgent need to explore them to resolve some of the ongoing debates in the literature about perceptual stability. For example, the frontal eye fields (FEF) and area V4 exhibit perisaccadic response field (RF) changes that have been implicated in perisaccadic perceptual mislocalization (Hamker et al. 2008, 2011; Tolias et al. 2001; Zirnsak et al. 2010; Zirnsak et al. 2014), although with some debate on the exact details of the mechanisms (Hartmann et al. 2017; Neupane et al. 2016a, 2016b). Moreover, even if there were no such debates, it is not known whether FEF or area V4 do exhibit upper/lower visual field asymmetries like the ones recently described in the SC (Hafed and Chen 2016). It is thus not yet known how our experimental results, described above, can emerge neurophysiologically. It would be highly interesting to use our results to motivate neurophysiological investigations that can pinpoint neural loci for perisaccadic perceptual mislocalization phenomena, and to specifically ask whether the SC is indeed relevant for these
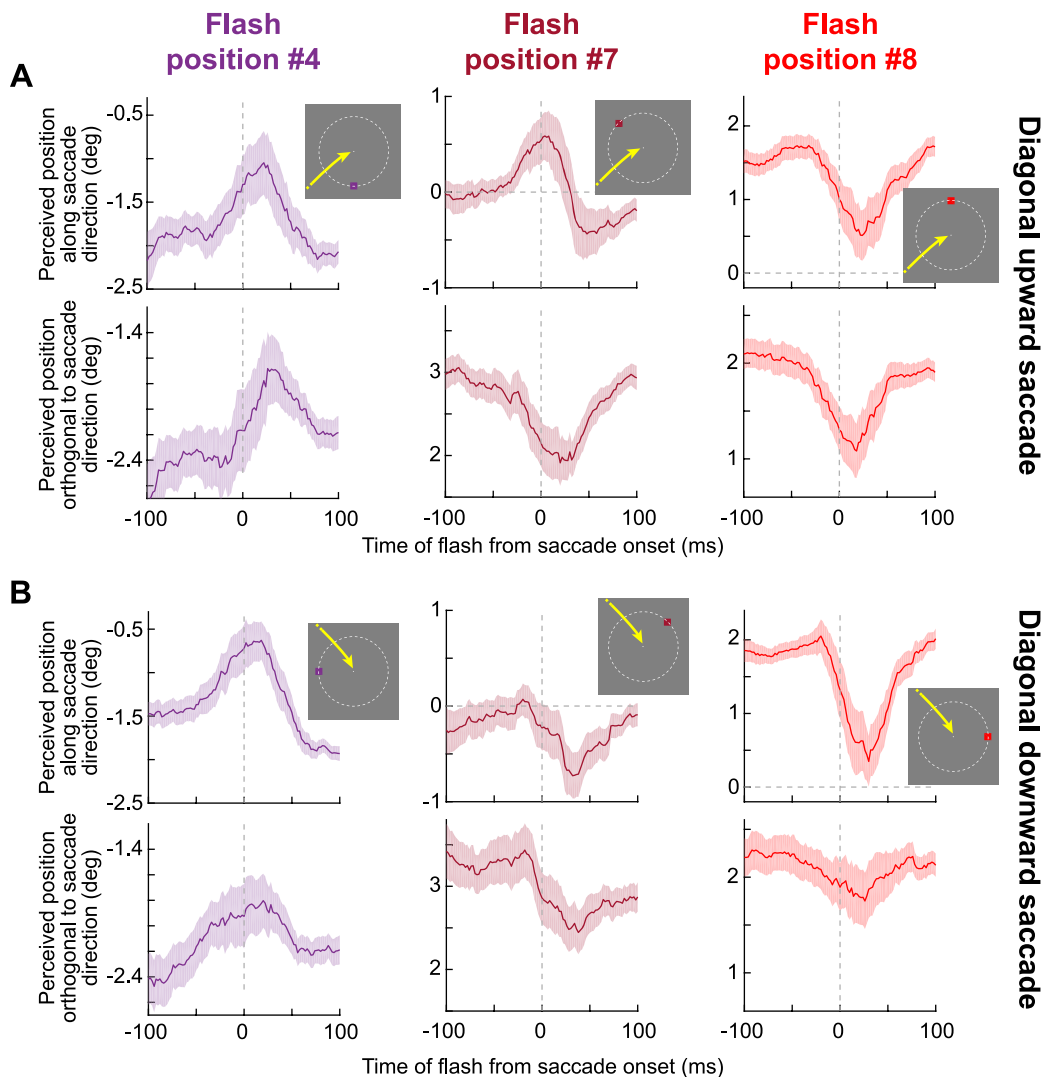
Fig. 11. Time courses of perceptual mislocalization for diagonal upward and diagonal downward saccades revealed interactions between saccade direction and flash location in the phenomenon of perisaccadic compression of space. *A*: a time course of perceived flash position plotted along (*top* row) or orthogonal to (*bottom* row) the axis of diagonal upward saccades for different flash locations (across columns). Error bars denote 95% confidence intervals. *B*: similar analysis for similar flash locations (relative to saccade direction and target location according to our standard convention) but for diagonal downward saccades. Accounts of compression based on the retinotopic eccentricity of the flash relative to the saccade target location predict identical patterns of parallel (along the axis of the saccade) and orthogonal mislocalization between corresponding flash locations in *A* and *B*. However, there were obvious differences based on saccade direction. For example, *flashes 7* and *8* showed more orthogonal mislocalization for the diagonal upward saccade than for the diagonal downward saccade. Mislocalization was strongest when both the saccade and the flash locations had upper visual field locations (i.e., *flashes 7* and *8*). In the time courses, $n = 57–116$ repetitions per time bin. *Insets* are schematics.

phenomena. These investigations must also pair neural recordings with behavior (in the same animals) to make the most sense. For example, in the other perisaccadic phenomenon of saccadic suppression alluded to in the INTRODUCTION, only when neurons have been linked to behavior in the same animals have certain perceptual properties of saccadic suppression found a convincing neural locus (Chen and Hafed 2017). It would also be interesting to further develop our conceptual modeling approach to a more quantitative one, which would be particularly useful if mislocalization were explored both behaviorally and neuronally in the same animals.

Having stated the above, it should be emphasized that our results and model so far do not unequivocally implicate the SC in perisaccadic perceptual mislocalization, although we do think that the SC might be involved given the details of our results. In our model and experiments, we simply used the SC

(Hafed and Chen 2016) as motivation for the idea that asymmetries in neural maps for upper and lower visual field representations can be relevant for perisaccadic perceptual mislocalization, and this was sufficient to uncover the observations that we have documented above. Neurophysiological experiments would be critically needed to investigate whether the SC is indeed relevant and how. Theoretically speaking, maybe even the asymmetry in relevant neural maps can be in the opposite direction from that in the SC and our model but still result in upward saccades being outliers with appropriate read-out mechanisms. However, we think that results such as those in Fig. 8 would suggest that the perceptual phenomenon likely does depend on maps with compressed lower rather than upper visual field representations. That is, if distortions in percepts for farther flash locations are due to compressed neural tissue at large eccentricities (Hamker et al. 2008, 2011;

Fig. 12. Asymmetries in perisaccadic mislocalization can occur if sensory-motor visual maps have asymmetries in their upper and lower visual field representations. *A* and *B*: it was suggested that patterns of 2-dimensional mislocalization (e.g., Fig. 1*A*) can arise as a result of translation of neural activity, on a visual map containing foveal magnification, from the peripheral locus, representing presaccadic target position, to the foveal locus, representing postsaccadic fixation. However, this account predicts similar mislocalizations regardless of saccade direction. We asked whether asymmetries in visual field representations can, theoretically, result in upward saccades having different perisaccadic mislocalization. We simulated a map having both foveal and upper visual field magnification (*A*) or a map having only foveal magnification but symmetric upper/lower visual fields (*B*). The equations for the maps are cited in MATERIALS AND METHODS. Also, the maps are oriented such that eccentricity is organized along the horizontal axis of neural tissue (curved vertical lines indicate isoeccentricity loci), and direction from horizontal is organized along the vertical axis (curved horizontal lines indicate isodirection loci; e.g., +45° and −45°). Horizontal or vertical saccades (squares), as well as their associated flash locations (colored circles), translate neural activity associated with the flashes toward the foveal origin of the map along the saccade trajectory (colored arrows). We used a simple translation along the axis of each saccade direction in the neural tissue. Because of foveal magnification, the resulting neural activity translated from the periphery (colored lines in the foveal region) is mislocalized relative to the veridical flash locations (black lines around the foveal region). Notice how a symmetric map (*B*) predicts similar mislocalization patterns for all saccade directions, whereas an asymmetric map (*A*) predicts that upward saccades would be outliers. *C* and *D*: similarly, a symmetric map (*D*) predicts similar mislocalization patterns for diagonal upward vs. downward saccades, but an asymmetric map (*C*) is more consistent with our observations of a difference in mislocalization between these otherwise identical saccades.
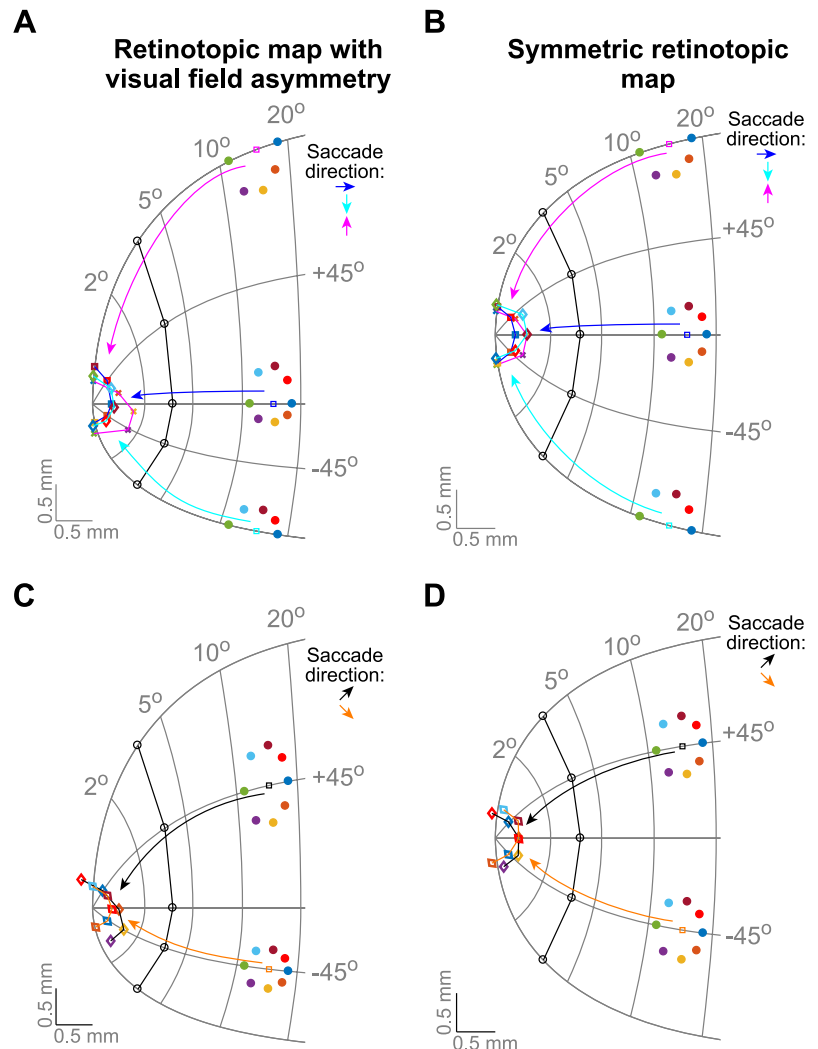
Kaiser and Lappe 2004; Richard et al. 2009; VanRullen 2004; Zirnsak et al. 2010), which increases uncertainty about true flash location, then the presence of orthogonal perceptual distortions for lower rather than upper visual field flash locations in Fig. 8 would argue, by the same logic, that the perceptual phenomenon depends on neural maps with compressed neural tissue for lower visual field locations, as in the SC (Hafed and Chen 2016).

It must also be emphasized that models other than the translation model, which we have highlighted as an example in Fig. 12, can also account for our results if asymmetries between upper and lower visual fields are introduced. Specifically, in such models (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et al. 2009; Zirnsak et al. 2010), mislocalization occurs because of an interaction between an oculomotor command in oculomotor maps and a visual response in visual maps. According to these models, specific patterns of mislocalization (e.g., Fig. 1*A*) arise, at least in part, because both the oculomotor and visual maps that are interacting exhibit foveal magnification. If these maps were to also exhibit other tissue asymmetries beyond foveal magnification, such as upper and lower visual field asymmetries, then interactions between them could still potentially account for our results. As

stated above, it would be interesting to understand how different maps exhibiting different amounts or types of magnification would need to be connected together to account for the asymmetries that we have observed in our current experiments.

Another intriguing aspect of our results is again related to Fig. 8, for which we found results apparently different from those of Kaiser and Lappe (2004) for horizontal saccades (at least for some flash locations). Specifically, we found that upper visual field flashes did not experience strong orthogonal mislocalization, whereas lower visual field flashes did. Although we do think that close inspection of their data reveals an asymmetry between upper and lower visual field flash locations consistent with our observations, it may be asked why the difference in Fig. 8 that we saw between upper and lower visual fields was stronger compared with their results. One possibility is that our saccades were slightly smaller than those used by Kaiser and Lappe (2004). With larger saccades, flashes and saccade targets are at more eccentric neural loci than with smaller saccades, which means neural tissue representing saccade and flash eccentricities is even more compressed compared with the case with smaller saccades. This naturally magnifies the mislocalization according to existing models (Hamker et al. 2008, 2011; Kaiser and Lappe 2004; Richard et

al. 2009; VanRullen 2004; Zirnsak et al. 2010). Thus, with our smaller saccades, we may have sampled different neural loci than Kaiser and Lappe (2004). It would be interesting to extend our and their results to different saccade amplitudes. Indeed, perisaccadic perceptual mislocalization still takes place for small saccades (Lavergne et al. 2010) and microsaccades (Hafed 2013).

Finally, we think that it would be interesting to explore reasons behind certain other observations in our data, such as the early bias in percepts for some flash locations in Fig. 6 well before any perisaccadic transient changes in perception started to occur. These biases, and our results overall, relate to asymmetries in several aspects of visual-motor behavior (Greenwood et al. 2017; Hafed and Chen 2016; He et al. 1996; Rubin et al. 1996), and understanding the commonalities and differences between these different phenomena would be important for pinpointing at which stage of visual processing perisaccadic perceptual mislocalization phenomena start to take place.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Z.M.H. conceived and designed research; N.G., N.B., C.G., W.Z., and Z.M.H. performed experiments; N.G., N.B., C.G., W.Z., and Z.M.H. analyzed data; N.G., N.B., C.G., W.Z., and Z.M.H. interpreted results of experiments; Z.M.H. prepared figures; Z.M.H. drafted manuscript; Z.M.H. edited and revised manuscript; N.G., N.B., C.G., W.Z., and Z.M.H. approved final version of manuscript.

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