

RESEARCH ARTICLE | *Control of Movement*

## Choosing a foveal goal recruits the saccadic system during smooth pursuit

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**Heinen SJ, Badler JB, Watamaniuk SNJ.** Choosing a foveal goal recruits the saccadic system during smooth pursuit. *J Neurophysiol* 120: 489–496, 2018. First published April 18, 2018; doi:10.1152/jn.00418.2017.—Models of smooth pursuit eye movements stabilize an object's retinal image, yet pursuit is peppered with small, destabilizing “catch-up” saccades. Catch-up saccades might help follow a small, spot stimulus used in most pursuit experiments, since fewer of them occur with large stimuli. However, they can return when a large stimulus has a small central feature. It may be that a central feature on a large object automatically recruits the saccadic system. Alternatively, a cognitive choice is made that the feature is the pursuit goal, and the saccadic system is then recruited to pursue it. Observers pursued a 5-dot stimulus composed of a central dot surrounded by four peripheral dots arranged as a diamond. An attention task specified the pursuit goal as either the central element, or the diamond gestalt. Fewer catch-up saccades occurred with the Gestalt goal than with the central goal, although the additional saccades with the central goal neither enhanced nor impeded pursuit. Furthermore, removing the central element from the diamond goal further reduced catch-up saccade frequency, indicating that the central element automatically triggered some saccades. Higher saccade frequency was not simply due to narrowly focused attention, since attending a small peripheral diamond during pursuit elicited fewer saccades than attending the diamond positioned foveally. The results suggest some saccades are automatically elicited by a small central element, but when it is chosen as the pursuit goal the saccadic system is further recruited to pursue it.

**NEW & NOTEWORTHY** Smooth-pursuit eye movements stabilize retinal image motion to prevent blur. Curiously, smooth pursuit is frequently supplemented by small catchup saccades that could reduce image clarity. Catchup saccades might only be needed to pursue small laboratory stimuli, as they are infrequent during large object pursuit. Yet large objects with central features revive them. Here, we show that voluntarily selecting a feature as the pursuit goal elicits saccades that do not help pursuit.

attention; eye movements; oculomotor; superior colliculus; target selection

### INTRODUCTION

Vision is limited by retinal factors that are compensated for by voluntary eye movements. For example, only the small fovea of the retina sees with high acuity (Hirsch and Curcio 1989), and saccades compensate for this limitation by rapidly moving the fovea to view scene details. Smooth-pursuit eye

movements compensate for another retinal limitation; when image motion on the retina exceeds 3°/s, the image blurs because of sluggish retinal dynamics (Westheimer and McKee 1975). The pursuit system is modeled as smoothly rotating the eyes to match target velocity (Krauzlis and Lisberger 1989; Robinson et al. 1986), a function that could prevent blur. Although the eyes generally do move smoothly with the target, frequent small, saccadic intrusions are nonetheless present. These “catchup saccades” supplement pursuit by correcting position and velocity errors between the eyes and a target (de Brouwer et al. 2002a). However, catchup saccades are not strictly beneficial, as they could compromise vision for several reasons. First, they rapidly reorient the eyes, causing the image to jump on the retina. Second, they mostly exceed 3°/s (e.g., see de Brouwer et al. 2002b), which is above the threshold for image blur (Westheimer and McKee 1975). Third, they reduce the perceived brightness of an image via saccadic suppression (Rucci and Mostofi 2017).

Whereas catchup saccades are common while pursuing small spot stimuli that are widely used in pursuit research, fewer of them occur while pursuing larger objects (Heinen and Watamaniuk 1998; Heinen et al. 2016). Larger pursuit stimuli also produce higher eye acceleration than does a spot (Heinen and Watamaniuk 1998; Watamaniuk and Heinen 1999, 2003). Higher eye acceleration with large objects might result from a stronger motion signal that they produce, and hence, fewer catchup saccades are required to help the pursuit system follow them. However, a stronger motion signal alone does not mitigate the need for catchup saccades, because although there are fewer of them while pursuing a large stimulus, they return when a small central dot is added to it (Heinen et al. 2016). Furthermore, the more numerous catch-p saccades with the added central element do not seem to improve pursuit, as they do not increase pursuit gain, nor do they better center the eyes on the stimulus (Heinen et al. 2016). Therefore, it appears that the additional saccades generated to a central element in a large stimulus are used to view or foveate the small central target and do not benefit pursuit per se.

If the extra saccades with the added central element did not benefit pursuit, why did they occur? The central dot might have been foveated automatically because small saccades correct position error between the fovea and a proximal small target. Alternatively, observers might have made a cognitive decision to pursue the central element instead of the larger stimulus. If so, the catchup saccades might be driven by not only position error but a combination of it and retinal slip, as occurs when a

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spot in isolation is pursued (de Brouwer et al. 2002a). Here, we test whether additional saccades occurred with a central target because of automatic position error correction, or a decision to pursue the central dot, by specifying either a foveal or a global pursuit goal on identical stimulus configurations. The stimulus was composed of five dots: one in the center and the other four arranged symmetrically around it in a diamond-shaped configuration, as in the previous study (Heinen et al. 2016). However, unlike in the previous work, in the current study the pursuit goal was specified. The goal was either the central dot, in which case observers detected a random dimming of it, or the diamond Gestalt, in which case they detect the dimming of a randomly specified peripheral dot. Catchup saccade frequency was higher when the goal was the central dot than when it was the diamond, evidence that the small goal preferentially recruited the saccadic system. Furthermore, catchup saccades with the central goal were more frequently associated with foveal position error than with velocity error. Even when the diamond was specified as the goal, removing the central dot further reduced catchup saccade frequency, indicating that a central dot can serve as a default goal and automatically recruit the saccadic system. Finally, a small pursuit goal in peripheral retina produced fewer catchup saccades than the same stimulus presented centrally, indicating that a small goal must be at the fovea to recruit the saccadic system.

## MATERIALS AND METHODS

**Subjects.** Four human observers (2 males, 2 females) participated in the experiments. *S2* and *S3* were naïve to the purpose of the study, *S1* was an author (S. N. J. Watamaniuk), and *S4* was a nonnaïve laboratory member. All had normal or corrected to normal vision and were between 24 and 50 yr old. The Smith-Kettlewell Institutional Review Board approved all experimental protocols, and all observers gave written, informed consent before participating.

**Apparatus and stimuli.** Visual stimuli were generated using functions from PsychToolbox (Brainard 1997; Kleiner et al. 2007; Pelli 1997) in MATLAB (Mathworks, Natick, MA) on a Macintosh G4 computer and were presented on a 17-inch, high-resolution Nanao color monitor (1.76 arcmin/pixel) with a refresh rate of 60 Hz. Horizontal and vertical eye position were sampled at 1,000 Hz by an EyeLink 1000 video-based eye tracker (SR Research, Mississauga, ON, Canada). The EyeLink was calibrated and validated before each block of trials using the standard nine-point method included with the system. Observers used a chin and forehead rest to stabilize the head and maintain a constant viewing distance of 48 cm.

**Stimuli and experimental procedure.** In the main experiment, stimuli were composed of five dots ( $0.2^\circ$  in diameter, luminance  $2.63 \text{ cd/m}^2$ ) presented on a dark background (luminance  $0.3 \text{ cd/m}^2$ ). The five-dot stimuli were arranged in a diamond configuration that had a radius of  $3^\circ$  (Fig. 1A). In each trial, the stimulus appeared on the left side of the screen for a randomized fixation period (between 500 and 1,000 ms), after which it translated from left to right for 1,500 ms at a randomly selected constant speed of either 10, 20, or  $30^\circ/\text{s}$ . Observers were instructed to follow the stimulus with their eyes, and they controlled the pace of the experiment by pressing the “Enter” key to initiate a trial. Each trial block (see below) contained a total of 108 trials, 36 at each speed. The data were pooled across stimulus speed since analyzing them separately produced the same results on our measures of interest.

We used a detection task to manipulate the pursuit goal on a single target configuration. For the small-goal condition (Fig. 1B, central task), only the central dot dimmed briefly (167 ms) at a random time (100, 300, or 500 ms after target motion onset) on 50% of the trials. Observers reported the dimming with a keypress. For the large-goal

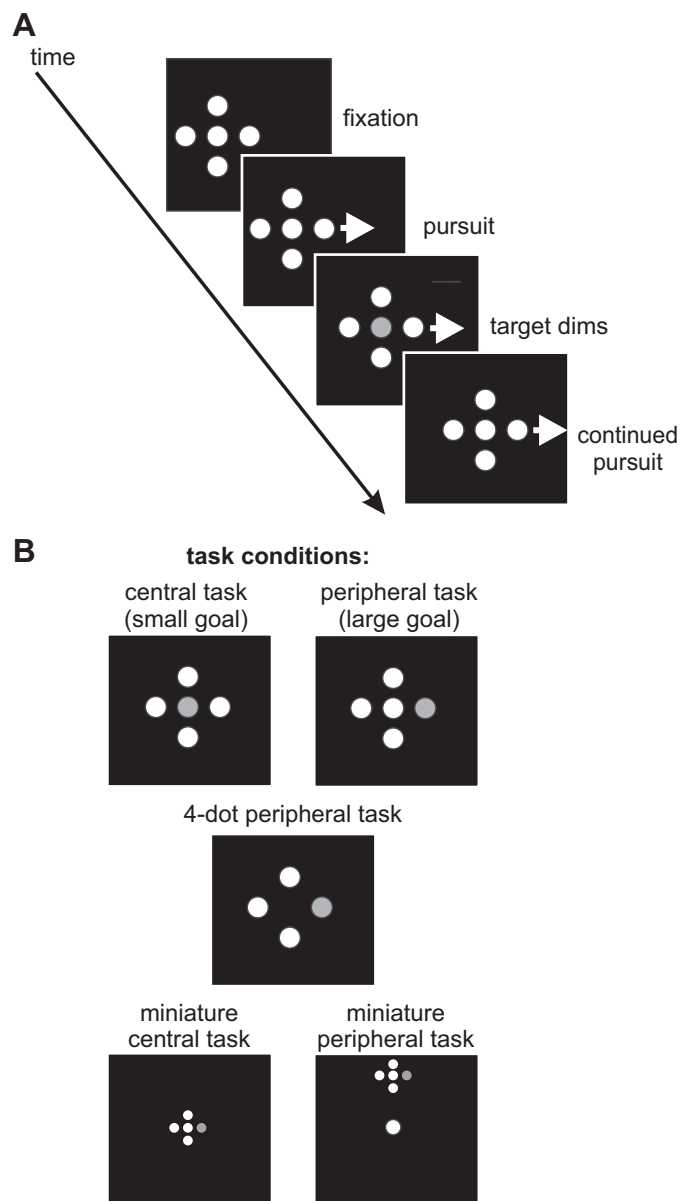


Fig. 1. Pursuit stimuli and task. *A*: the central task (small goal) condition in the main experiment. Subjects pursued the dot array and indicated whether the central dot dimmed. *B*: task conditions. Central task as above. In the peripheral task (large goal), 1 of the 4 peripheral dots dimmed. The 4-dot peripheral task was like the peripheral task, but the central dot was absent. In the miniature central and miniature peripheral tasks, a  $0.5^\circ$  version of the 5-dot array was presented either centered or above the center in the periphery. Observers identified which of the 5 dots dimmed. Note that all panels are schematic only; dot size and position are not to scale.

condition (Fig. 1B, peripheral task), one of the four peripheral dots chosen randomly dimmed on every trial, and observers identified it with a keypress. Before the experiment, the dimming level was customized for each observer to yield a 75% detection rate on a static stimulus.

In the first control experiment, only the four-dot stimulus was presented (Fig. 1B, 4-dot peripheral task). As with the peripheral task, a dimming could occur on any of the four dots, and a dot dimmed on every trial. As before, observers identified which dot dimmed with a keypress. In the second control experiment, observers performed the discrimination on a miniature five-dot stimulus ( $0.2^\circ$  total diameter,  $0.03^\circ$  dot diameter) that was either positioned in the center (miniature

central task) or 6° above a central spot (miniature peripheral task) that translated along with it at the same velocity. Any one of the five miniature dots dimmed on every trial, and that dot again was identified with a keypress. Observers performed the discrimination while they pursued the central element with the fovea, either the miniature array or the spot. A chi-squared test ( $df = 1$ ) was used to compare overall subject performance between tasks.

**Eye movement analysis.** Horizontal and vertical eye velocity were calculated offline from the recorded eye position signals by differentiating and filtering the raw position data (2-pole Butterworth filter, cutoff = 50 Hz). Saccades were detected using the EyeLink automatic saccade detection routine and its standard parameters (displacement threshold: 0.1°; velocity threshold: 30°/s; acceleration threshold: 8,000°/s<sup>2</sup>). An experienced operator inspected all horizontal and vertical eye velocity traces to find missed and false-positive saccades. Missed saccades were corrected by manually selecting their start and end points, and false positives were rejected. Saccades were replaced in the velocity traces by a linear interpolation to facilitate pursuit detection. Pursuit onset was first detected automatically by computing the mean and standard deviation over a sliding 100-ms window and checking for points that exceeded thresholds of 5°/s and 20°/s<sup>2</sup>, respectively. The resulting onset times were then adjusted manually if a significant disconnect was apparent between when the eyes began to accelerate from baseline and the automatic detection result.

**Catchup saccade analysis.** Catchup saccades were quantified during steady-state pursuit to avoid both the large saccades that occur following pursuit onset and those that might anticipate the end of the trial. These considerations resulted in using a steady-state interval that began 130 ms after pursuit onset and had a fixed length of 500 ms. Trials without a clearly identifiable pursuit onset were excluded from the analysis (<1% for all conditions). Only saccades that began during the steady-state interval were counted. For each subject and experiment, the average saccade frequency was obtained by dividing the total saccade count by the sum of all interval durations. To construct error bars, 95% confidence intervals were computed using a bootstrap method: trials were randomly selected with replacement 10,000 times to generate a bootstrap distribution of saccade counts. The 2.5th and 97.5th percentiles were then computed to obtain the confidence intervals. A chi-squared test ( $df = 1$ ) was used to check whether a given pair of conditions had significantly different saccade rates across all subjects, and a binomial test was used to check the difference for each subject individually. An  $\alpha$  of 0.05 was used for all statistical tests.

**Determining contributions of sensory cues to catchup saccades.** A second analysis was performed to determine the sensory cues contributing to steady-state catchup saccade generation based on the method of de Brouwer et al. (2002a). Briefly, the method calculates the probability that a saccade will occur for a given value of position error (PE) and retinal slip (RS). For each saccade identified in the steady-state interval, PE and RS are calculated in a 50-ms window centered 125 ms before saccade onset. This is approximately the interval during which these errors contribute to generating a catchup saccade (de Brouwer et al. 2002a). Within the window, PE and RS are computed by subtracting the horizontal components of the target from the eye position and velocity, respectively. This yields a signed quantity that is negative when the eye is behind or slower than the target and positive when the eye is ahead of or faster than the target. Target position was taken as the centroid of all dot positions. We used only the horizontal component in the analysis since target motion was constrained to the horizontal axis.

The saccade probability computation also requires a set of sensory error values that do not evoke a saccade. In the original de Brouwer et al. (2002a) experiment, saccades did or did not occur following discrete changes in target motion. Because the saccades in our study were not linked to a single stimulus perturbation and could occur anywhere in the analysis interval, we used a bootstrap procedure to generate a distribution of error values that did not result in a saccade.

First, for each subject and condition, we took each trial without a saccade and calculated position error (PE<sub>NS</sub>) and retinal slip (RS<sub>NS</sub>) using the entire set of saccade onset times from the rest of the trials. Saccades were corrected for pursuit latency of the trial in which they occurred, and the same analysis window (50 ms centered 100 ms before saccade onset) was used to compute the errors. Next, the PE and RS values for saccade trials were grouped into eight bins, using all subjects. PE<sub>NS</sub> and RS<sub>NS</sub> values were then drawn randomly with replacement from the sets calculated in the first step and sorted into the same bins, a process repeated 10,000 times. To keep the overall probability of generating a saccade consistent for each condition, the number of no-saccade error values drawn was equal to the number of saccade error values multiplied by the ratio of no-saccade trials to saccade trials. Each error bin thus contained a distribution of saccade probabilities, calculated as  $n_i \text{PE} / (n_i \text{PE} + n_i \text{PE}_{\text{NS}})$  and  $n_i \text{RS} / (n_i \text{RS} + n_i \text{RS}_{\text{NS}})$ , where  $n_i$  denotes the number of error values in the  $i$ th bin. The median probability is the 50th percentile of the distribution, and the 95% confidence interval is the range between the 2.5th and 97.5th percentiles.

## RESULTS

Catchup saccades are generally thought to be automatically generated as a consequence of position and velocity error between the stimulus and the eyes (de Brouwer et al. 2002a). Furthermore, their frequency is significantly reduced when large stimuli are pursued (Heinen and Watamaniuk 1998), suggesting that large stimuli might minimize position and velocity errors. However, saccades return when a large stimulus has a distinct central component (Heinen et al. 2016). This might be because the central component becomes the pursuit goal, and like a small spot in isolation, it recruits the saccadic system, which generates catchup saccades.

In the main experiment, we investigated using the same large stimulus whether the saccadic system was differentially recruited when the pursuit goal was specified as either the large Gestalt or the small central element. Observers pursued a five-dot stimulus with four symmetrical peripheral dots arranged as a diamond around a central one (see Fig. 1). To specify the goal, in separate blocks one of two tasks was imposed on the stimulus, a central task, or a peripheral task. In the central task, we specified the central target as the pursuit goal by having observers detect when it briefly dimmed. In the peripheral task, we specified the Gestalt diamond as the pursuit goal by having observers detect a brief dimming of one of the peripheral dots. All observers performed correctly at rates from 90 to 94% for the central task and 72 to 83% for the peripheral task ( $\chi^2 = 7.101$ ,  $P < 0.01$ ). Figure 2A shows raw eye velocity traces from one observer in the two conditions. When the central target was the goal, more catchup saccades occurred than when the gestalt object was the goal. The difference was consistent across all observers (Fig. 2B), and significant both overall ( $\chi^2 = 33.281$ ,  $P < 0.001$ ) and individually (binomial test,  $P < 0.015$ , 0.001, 0.001, and 0.022 for *S1*, *S2*, *S3*, and *S4*, respectively). There was no significant difference in saccade magnitude or pursuit gain between the two conditions (Mann-Whitney test,  $P > 0.05$  for all; Fig. 3), suggesting that the change in saccade frequency neither aided nor impeded smooth pursuit.

Could sensory cues have evoked the additional saccades with the central pursuit goal? Our previous work showed that when an isolated spot target is pursued, catchup saccades are preferentially generated to correct for position error between the spot and the fovea, as opposed to correcting for motion

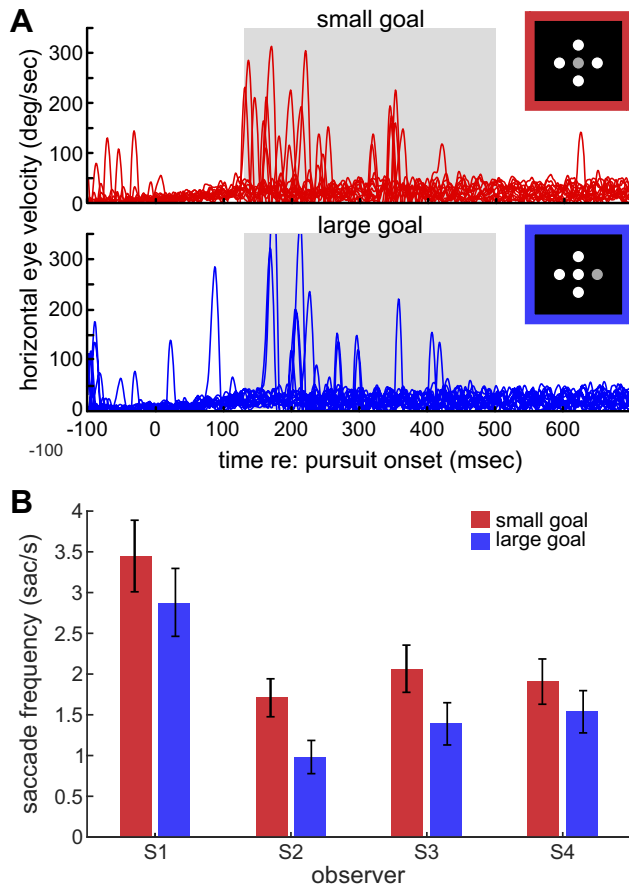


Fig. 2. Catchup saccades with small- and large-pursuit goals. *A*: superimposed eye velocity traces (5/target speed, selected randomly) aligned on pursuit onset for a single subject (*S4*) in the central and peripheral task conditions. The shaded regions denote the analysis period. *B*: summary data for all subjects show consistently more saccades for the central than for the peripheral conditions. Error bars show 95% confidence intervals by bootstrap.

error, or retinal slip (Heinen et al. 2016). We thought that when the central element was chosen as the pursuit goal, it might activate position and retinal slip mechanisms similarly as during pursuit of an isolated spot. To determine this, we compared the relative position error (PE) and retinal slip (RS) preceding steady-state catchup saccades in both conditions (see MATERIALS AND METHODS). Figure 4*A* shows scatterplots of RS vs. PE for all subjects for the small- and large-goal conditions. There was a small difference in median PE (small goal = 0.24, large goal = -0.08; Mann-Whitney test,  $P = 0.04$ ) but no difference in median RS ( $P = 0.6$ ). To assess how the probability of making a saccade varied across the range of PE and RS values, we used the bootstrap procedure described in MATERIALS AND METHODS.

Relative to the small goal, the large goal significantly decreased saccade probability for small values of PE (Fig. 4*B*) and RS (Fig. 4*C*), as evidenced by the nonoverlapping 95% confidence intervals that correspond to uncorrected  $P$  values of  $<0.05$ . By contrast, for PE values  $<2.5^\circ/s$  and RS values  $<15$  or  $>10^\circ/s$ , the probability curves overlapped. That is to say, large tracking errors tended to evoke catchup saccades regardless of the goal condition, but the small goal made saccades more likely in response to small tracking errors.

Our results show that catchup saccades were reduced when the large, Gestalt object of the five-dot stimulus was specified

as the pursuit goal. This occurs despite the fact that the stimulus had a central element, a condition that increases catchup saccades when a pursuit goal is not explicitly specified (Heinen et al. 2016). Could the mere presence of a central element still elicit some catchup saccades because of its proximity to the fovea despite the fact that the Gestalt object is selected as the pursuit goal? To test this, we compared pursuit in two conditions that each specified the large four-dot diamond as the goal. Both conditions used the same peripheral task as before in which one of the peripheral dots dimmed. In the first condition, the central dot was present, and in the second condition, the central dot was absent (see Fig. 1*B*). Subjects 1–4 performed with an accuracy ranging from 62 to 86%, which was not different from the large goal condition in the main experiment (chi-square test,  $P = 0.7$ ). The saccade frequency results are shown in Fig. 5. The absence of the central dot further reduced steady-state catch-up saccades overall ( $\chi^2 = 26.450$ ,  $P < 0.001$ ) and in three of four subjects (binomial test,  $P > 0.7$  for *S1*;  $P < 0.001$ , 0.001, and 0.006 for *S2*, *S3*, and *S4* respectively). The results suggest that a small central stimulus can serve as the default pursuit goal even when not specified as such.

To specify the small target goal in the central task of the main experiment, we required subjects to focus attention on a central element within a large stimulus. We attributed the increase in saccade frequency to the choice of a central pursuit goal. Alternatively, saccade frequency was higher because attention was more narrowly focused in the central task than in the peripheral task. In other words, narrowly focused attention at any spatial location might be sufficient to recruit the catchup saccade mechanism, and a foveal attention locus is not required. To test whether focused attention deployed at a different location than the fovea could recruit the catchup saccade mechanism, we looked at catchup saccade frequency while observers performed a discrimination on a small stimulus in the periphery during pursuit. The discrimination stimulus was a miniature version of the main task stimulus (see Fig. 1*B*), a five-dot array with only a  $0.5^\circ$  radius (see MATERIALS AND METHODS). In the peripheral condition, the miniature stimulus was placed  $6.0^\circ$  above a central spot, and observers pursued the central spot while both elements translated across the screen together. The stimulus was aligned vertically to avoid the confound of horizontal attention displacement during pursuit (e.g., Khan et al. 2010), but the choice of up (vs. down) was arbitrary.

Catchup saccade frequency in the peripheral condition was compared with that obtained in a central condition when observers pursued a centrally presented miniature stimulus. In both conditions, observers identified which of the five dots dimmed. The focus of attention required to perform the task was thus identical in both conditions; only the attended retinal location differed. Performance was no different for the central and peripheral tasks and ranged from 73 to 78% for the central task and 66 to 72% for the peripheral task (chi-square test,  $P = 0.3$ ). However, analogous to the main experiment, the central task evoked more saccades than the peripheral one (Fig. 6), both overall ( $\chi^2 = 59.586$ ,  $P < 0.001$ ) and for all individual subjects (binomial test,  $P < 0.012$ , 0.001, 0.001 and 0.007 for *S1*, *S2*, *S3*, and *S4*, respectively). Therefore, the increase in catchup saccades depended critically on the presence of a foveal goal and was not an artifact of the scope of attentional focus.

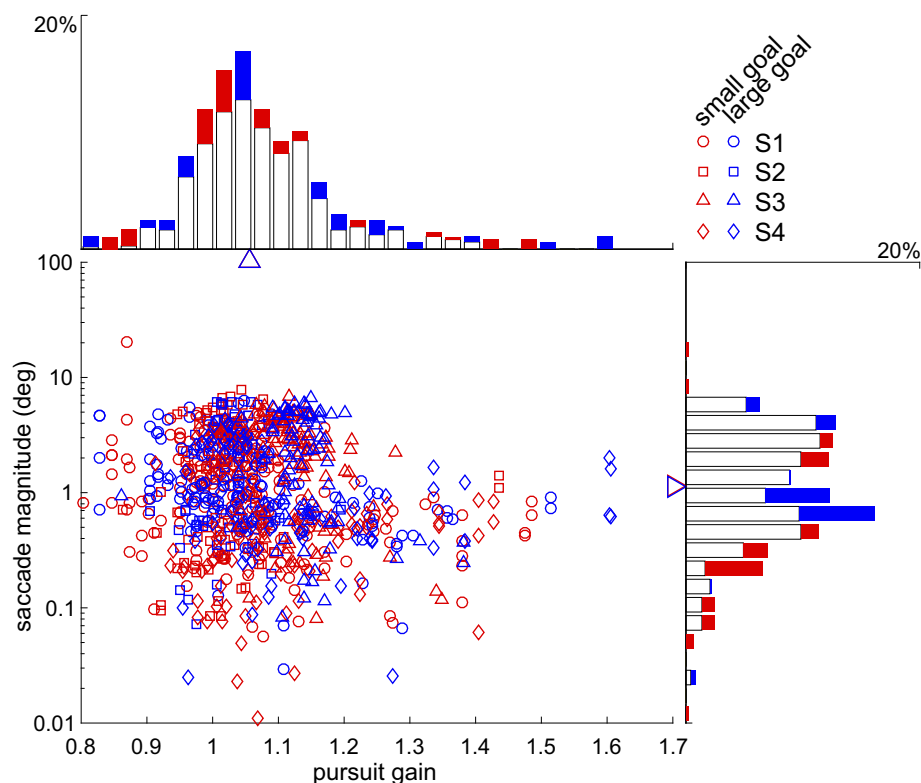


Fig. 3. Saccade magnitude versus pursuit gain for large and small goals. Each data point represents 1 saccade. The marginal histograms show the percentage of trials for each goal condition. Triangles indicate the medians; white color signifies overlap. No significant differences between the small- and large-goal conditions were found.

## DISCUSSION

We presented observers with a large diamond-shaped stimulus with a central dot and specified the pursuit goal as either the diamond Gestalt or the central dot using a dot-dimming task. We found that when the central dot was the goal, catchup saccade frequency was higher than when the diamond was the goal, indicating increased recruitment of the saccadic system. When we removed the central dot from the attended diamond, saccade frequency decreased below the level observed when it was present. Analyzing the sensory cues that preceded catchup saccades suggested that catchup saccades predominantly corrected for position error, but more so when the goal was the central dot. In a control experiment, observers performed an attention-demanding task on the same small stimulus positioned either centrally or peripherally during pursuit. Saccade frequency was higher for the central stimulus, discounting the possibility that the higher saccade frequency with the central pursuit goal was solely the result of a narrower attentional focus.

Smooth-pursuit eye movements are usually studied with a small spot stimulus. A prominent feature of spot pursuit is the presence of catchup saccades, small saccadic intrusions that occur with a frequency of about two per second (e.g., Heinen et al. 2016). Although other work has investigated sensory cues that trigger them (de Brouwer et al. 2002a; Heywood and Churcher 1981; Keller and Johnsen 1990), their purpose is not known. Ostensibly, and implicit in their name, they occur to supplement pursuit gain when it is less than 1.0, possibly because a spot stimulus creates a weak motion signal (Jazayeri and Movshon 2007; Tsumishima 2014). Consistent with the idea that catchup saccades compensate for the weak motion signal of a spot, large-pursuit objects, which presumably create a stronger motion signal, produce fewer catchup saccades (Hei-

nen et al. 2016; Heinen and Watamaniuk 1998). However, recent work suggests that a stronger motion signal is not the only reason that fewer catchup saccades occur with large stimuli, as large-pursuit stimuli with a central component dot produce almost as many saccades as does a single dot (Heinen et al. 2016). That work further demonstrated that catchup saccades are used mostly to foveate an isolated dot during pursuit or to foveate the central dot in a large pursuit stimulus.

The large stimulus in the Heinen et al. (2016) study was composed of multiple dots, any of which could have evoked a foveating saccade during pursuit. Why did the central dot in particular recruit the saccadic system? There are two simple mechanistic explanations for more saccades with the central dot. One is that a centrally located feature helps keep the fovea at the center of mass during pursuit, which is analogous to how saccades target the center of mass of a large stimulus (McGowan et al. 1998). Another is that the saccadic system automatically corrects for a spot's position error if that spot is near the fovea. However, neither explanation fully accounts for our results, as there was a central spot in both the central and peripheral detection tasks, yet saccades were higher during the central task. Our results suggest that an additional process generates catchup saccades when a large pursuit stimulus has a central spot. The saccadic system may be recruited to assist in attentive foveation of a central goal, since saccades primarily foveate (Fuchs et al. 1985; Van Gisbergen et al. 1981), and attention and the saccadic system are linked (e.g., see Kowler et al. 1995 and McPeck et al. 1999). Attentive foveation might occur in parallel with the smooth eye velocity generation, explaining why it does not affect pursuit gain. Conversely, pursuing a large stimulus with attention directed peripherally does not elicit foveation, and fewer saccades result.

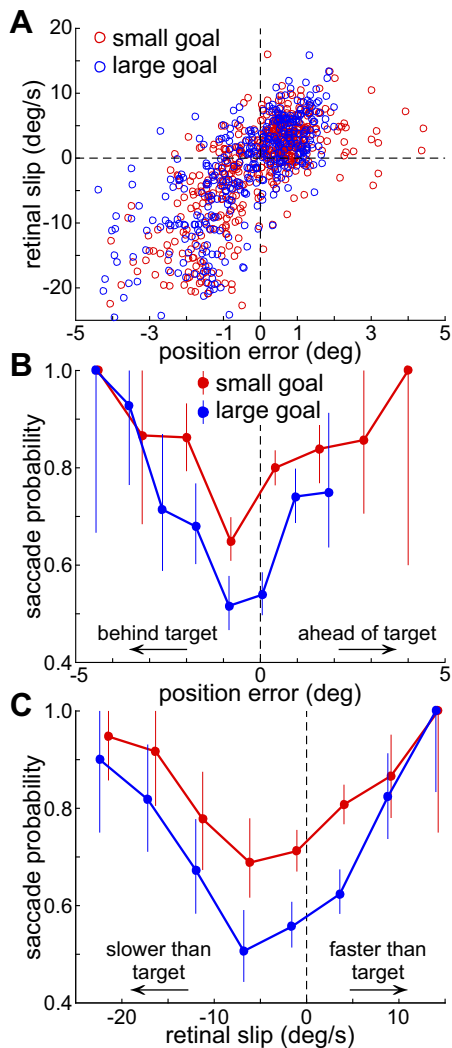


Fig. 4. Contribution of position and velocity error to catchup saccades is identical for large and small goals. **A**: signed retinal slip versus position error centered 125 ms before saccade onset for the small (red) and large (blue) goals. Each data point represents 1 saccade. **B**: probability of evoking a saccade for a given position error for both conditions. Error bars show 95% confidence intervals, as computed by bootstrap; see MATERIALS AND METHODS for details. **C**: probability of evoking a saccade for a given retinal slip. Other details are as shown in **B**.

Notably, the mere presence of a central dot was sufficient to increase saccade frequency despite the fact that the dot was not specified as the pursuit goal. Therefore, some of the saccades recruited by a central stimulus might subserve mechanistic centering or position correction. More saccades when a central spot is present might also reflect a training effect; i.e., experience with pursuing a spot could bias observers to choose it as the default goal. In support of this explanation, all of our naive observers were trained in spot pursuit, since we find that pursuit gain in humans is low without training, as it is in monkeys (Bourrelly et al. 2016).

Whereas choosing a large pursuit goal reduced the frequency of catchup saccades, it did not eliminate them. This allowed us to test whether different factors contributed to generating the saccades while pursuing large and small goals. Although the saccadic system corrects position error between the fovea and a pursuit target, catchup saccades during pursuit are also driven by the velocity error, or “retinal slip” (de Brouwer et al. 2002a;

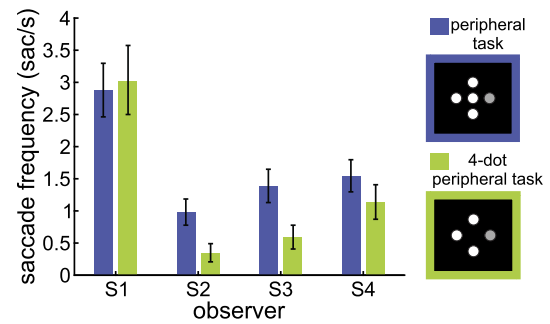


Fig. 5. Catchup saccade frequency with and without a central element. The mere presence of the central dot increased saccade frequency. In both conditions, the task was on the 4 peripheral dots.

Heywood and Churcher 1981; Keller and Johnsen 1990). In our study, the proportion of saccades driven by position error, as well as by retinal slip, was greater with the small goal than with the large goal. However, saccade frequency with the large and small goals was only different for small error values; large values of either position error or retinal slip were equally probable in generating a saccade regardless of condition. Because pursuit gain was also unaffected by the goal choice, the additional catchup saccades occurring with the small-pursuit goal apparently did not supplement the pursuit drive. Instead, a small goal seems to increase the sensitivity of the saccadic system to correct sensory errors.

The Gestalt goal produced a position error that was a vector average of its components, and that position error might have triggered catchup saccades even if they did not foveate a dot element. It is also possible that some catchup saccades accompanying the Gestalt goal resulted from observers attending to the peripheral dots composing the Gestalt goal. In support of this, fixational microsaccades point in the direction of stimuli that are cued (Engbert and Kliegl 2003; Hafed and Clark 2002; Pastukhov and Braun 2010) or are linked to endogenous attention when observers attend stimuli that are not overtly cued (Yuval-Greenberg et al. 2014). Still, there were fewer saccades while pursuing the Gestalt than while pursuing the central goal. This may be because a central goal requires more focused attention. However, focused attention alone cannot account for the saccade rate increase, because fewer saccades occurred in our miniature stimulus control experiment when attention was focused in the periphery. Therefore, focused attention on a specifically foveal goal seems essential for increased saccade frequency. We found that more catchup saccades occurred when small, foveal stimuli were the pursuit goal, even though these additional saccades did not improve

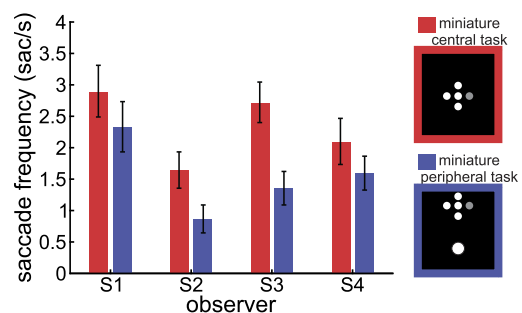


Fig. 6. Testing focused attention with a miniature peripheral task. Saccade frequency was lower when the task was performed on a miniature array in the periphery than when the identical array was positioned centrally.

pursuit. This could explain why neural saccade structures are active while small targets are pursued in isolation, which is presumably the pursuit goal by default (for a review see Keller and Heinen 1991; Krauzlis 2004). However, in studies that implicate saccade structures in smooth-pursuit control, neurons in that structure are routinely tested to determine whether they remain active during epochs of smooth eye velocity when no saccades occur [e.g., the superior colliculus (Krauzlis et al. 2000) and the supplementary eye field (Heinen and Liu 1997)]. It is possible that during saccade-free epochs, saccade structures still contribute to smooth eye velocity during pursuit via a position signal that is subthreshold for triggering a saccade. In support of this, there is behavioral evidence that position error contributes to smooth eye velocity (Blohm et al. 2005; Pola and Wyatt 1980). A position contribution to pursuit is also neurally plausible, given that at least in the colliculus, a key saccade structure, position error is encoded (Waitzman et al. 1988). Such error signals would putatively contribute to the velocity drive when they are below the threshold to generate a saccade but generate a saccade when that threshold is crossed. Therefore, catchup saccade frequency could serve as a proxy of the degree to which the saccadic system is recruited during pursuit.

The converse might also be true, that saccade structures tend to be silent when a large object is the pursuit goal. The current study and other work (Heinen et al. 2016; Heinen and Watamaniuk 1998) show that fewer saccades occur during pursuit of large stimuli. If catchup saccade frequency is a proxy for saccade structure recruitment, fewer saccades would indicate less activity in those structures. In fact, saccade structures may be completely quiescent if the putative subthreshold saccadic signal for correcting position error is unnecessary to pursue large stimuli. Instead, when larger objects are the pursuit goal, pursuit may take its input exclusively from motion structures such as MT and MST (Komatsu and Wurtz 1988; Newsome et al. 1988).

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#### DISCLOSURES

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

#### AUTHOR CONTRIBUTIONS

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

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