

Frequency and Metrics of Square-Wave Jerks: Influences of Task-Demand Characteristics

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PURPOSE. Square-wave jerks (SWJs) during visual fixation and pursuit tracking of targets of varying speed and predictability were investigated in the present study.

METHODS. SWJs were measured in 91 subjects as they fixated a target or a remembered target location and tracked targets that varied in velocity and predictability.

RESULTS. Percentages of subjects making SWJ and mean SWJ frequency per minute in the high- and low-predictability conditions were 99% and 9.34 and 91% and 2.78, respectively. SWJ rates were significantly lower when observers fixated remembered target locations rather than visual targets and during tracking of faster-moving and less predictable targets. Differences in task conditions cannot be explained by volitional influences to control the first saccade in the SWJ. There was also no influence of age on SWJ rate.

CONCLUSIONS. Reduced SWJ rates after manipulations that increased task demands on visual pursuit of targets suggest an inverse relationship between current demands imposed by visual tasks and rates of intrusive saccades. These findings suggest that signals from cortical attentional systems may suppress inappropriate saccades that would divert the eyes from objects of interest during conditions imposing high task demands on the visual system. (*Invest Ophthalmol Vis Sci.* 2003; 44:1082-1087) DOI:10.1167/iovs.02-0356

Square-wave jerks (SWJ) are pairs of saccades: the first a saccade taking the eyes off target and the second a corrective saccade bringing the eyes back to the target.^{1,2} There is a range of SWJs among normal adults.³⁻⁵ High rates of SWJ are associated with multiple neurologic disorders, including Friedreich's ataxia^{6,7}; Huntington's chorea⁸; multiple sclerosis⁹; acute encephalopathy¹⁰; Parkinson's disease,¹¹ especially in the Parkinsonian disorder, progressive supranuclear palsy¹²; and after pallidotomy in Parkinsonian patients.¹³

The prevailing view in the clinical literature is that the first saccade in an SWJ is an involuntary act due to a failure of inhibitory control of brain stem saccade generators, as, for example, might result from a temporary lapse in inhibitory control of omnipause cells over saccadic burst neurons in the

brain stem.¹⁴ A potential source of this inhibitory control is the frontal eye fields, which are believed to play a major role in suppressing nonpurposeful saccades through inhibition of the superior colliculus (SC)^{15,16} and excitation of omnipause neurons in the brain stem.¹⁷ Another source is the basal ganglia.¹³ Saccade-related cells within SC are under tonic inhibition by cells in the substantia nigra pars reticulata, an output pathway of the basal ganglia.^{18,19} This suppression of context-inappropriate saccades such as SWJs could have the adaptive advantage of helping to maintain foveation of targets of interest. This model of SWJ predicts that the rate of their occurrence varies with attentional demands (i.e., varying predictability and stimulus velocity) through facilitation of top-down cortical control of eye movements, but this has not been tested. Although it has been shown that normal adults exhibit SWJs^{3,5} and that the frequency and size of SWJs vary with age,⁴ to our knowledge there have been no investigations directly testing the impact of relevant task demands on the effective suppression of intrusive saccades.

We first sought to test whether the frequency of SWJs in a large group of normal adult subjects naïve to eye movement studies would vary with changes in predictability and stimulus velocity during pursuit-tracking tasks that impose various degrees of processing demands (e.g., effort, concentration, and resources including attention). Subjects are known to track low-predictability targets²⁰⁻²³ and faster-moving targets less accurately,^{24,25} presumably increasing effort, concentration, and overall demands on the eye movement system to attempt to track such targets accurately. The first study was designed to determine whether decreasing target predictability and increasing target speed would be associated with a reduction in the frequency of SWJs.

A second question that we investigated is whether SWJs are similar to voluntary efforts to look away from visual targets during pursuit and fixation tasks. The possibility that SWJs might be voluntary shifts of gaze rather than intrusive saccades resulting from a disinhibition of brain stem saccade generators is raised by reports that observers are able to suppress saccades during maintained fixation when told to do so,²⁶ that the rate of saccades is dependent on the subject's level of interest in the task,²⁷⁻²⁹ and that subjects can choose to make frequent saccadic position corrections, sometimes completely depending on what they had been instructed to do.²⁶ To control for the possibility that some or all subjects can make voluntary saccades that may result in differences among task conditions, we conducted a second study testing whether subjects can voluntarily make pairs of saccades that match the metrics of involuntary SWJs.

METHOD

Subjects

Ninety-one healthy subjects 18 to 56 years of age with normal or corrected-to-normal vision and naïve to eye movement studies were tested in the first study. Authors DS and JS served as subjects in the second study that tested voluntary versus involuntary SWJs. Informed consent was obtained from all subjects. The rules outlined by the Declaration of Helsinki were followed.

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Procedure

Subjects sat 1 m from a 1-m radius acrylic hemiarc at eye level in a darkened room painted optical flat black. A chin rest with occipital support secured the head and a head strap minimized head movement. A 3-mm diameter point source of light was projected onto the hemiarc, using a servo motion controller (model 1121-080S; NEAT 310S; Danaher Precision Systems, Salem, NH).

Oscillating Target-Tracking Task

A visual tracking task with an oscillating stimulus was used to assess SWJ rate during pursuit of highly predictable stimuli. The target began at center (0° visual angle) and swept first at a constant velocity to the left, slowing at -12° to a stop at -17° of visual angle. On reaching zero velocity at -17° , the target immediately reversed direction, accelerating to achieve the desired speed as it reached -12° . Target velocity was constant between $\pm 12^\circ$, after which the target gradually decelerated until reaching 0 deg/sec at $\pm 17^\circ$. At that point, it immediately began moving back across the arc, accelerating until it reached $\pm 12^\circ$. SWJs were measured only between $\pm 10^\circ$ of visual angle, during which time the target was moving at a constant predictable velocity. The onset of the stimulus presentation was preceded by an auditory cue presented 2 seconds before the start of each block of trials. Subjects were told that a light would start at center and then move smoothly back and forth across the screen. Subjects were instructed to follow the light as closely as possible. This oscillating target task has predictability features similar to those of an oscillating sinusoidal waveform but has the advantage that adjustments for dynamic changes in target velocity and acceleration are not needed during the period when tracking performance is evaluated.

Target velocities of 8, 16, 24, and 32 deg/sec were used. The target velocities were put into slow, medium, and fast categories with 8, 16, and 24 deg/sec being the slow, medium and fast speed categories to match three similar target velocities in the ramp task as discussed in the next section.

Ramp Task

A ramp task was used to assess SWJ rates during visual tracking of less-predictable stimuli. Ramp targets began at center (0° visual angle) and swept either leftward or rightward 15° at a constant velocity. The target was extinguished once it reached $\pm 15^\circ$ from center fixation, to obtain the maximal amount of pursuit within the linear range of the eye movement monitoring system. Ramp targets began at center fixation to minimize anticipation of the direction of target movement. Eight trials were presented at each target speed and were split equally between the directions in which the target moved (left-right) using a fixed pseudorandom trial format. Target speeds were also presented in a fixed pseudorandom format. Thus, subjects did not know when the next trial would begin, nor in what direction or at what speed the target would move.

Target velocities used were 4, 8, 14, 20, and 26 deg/sec. Target speeds were lower in the ramp than the oscillating task because of the greater difficulty in accurately tracking such unpredictable ramp targets compared with that of tracking oscillating targets.³⁰ The target speeds of 8, 14, and 26 deg/sec made up the slow, medium, and fast categories for the ramp condition.

Fixation Tasks

SWJ rates were also compared in two fixation tasks. Subjects fixated a target and then fixated a remembered target location. We expected SWJ rates during fixation of a remembered target location to be lower than during fixation of a visual target that had no task demand except keeping the eyes focused on a target.

Fixation to Target. Subjects were instructed to fixate a central cue for 15 seconds.

Fixation to Remembered Target Location. After the subjects fixated a central cue for 15 seconds, the central fixation point was extinguished. Subjects were then immediately instructed to continue

fixating the location where the central target had been (without its actually being present) for another 15 seconds (i.e., fixation in the dark).

Eye Movement Measurement and Analysis

Eye movement recordings were obtained using infrared (IR) scleral-reflection sensors mounted on spectacle frames (Model 210; Applied Science Laboratories, Inc., Bedford, MA). Sensor signals were digitized on-line at 500 Hz (Dataq Instruments, Akron, OH). An SWJ was defined as comprising a small ($\leq 3^\circ$) initial saccade away from the target followed by a second saccade in the opposite direction that refoveated the target, similar to other researchers.¹ The second saccade had to follow the first by at least 100 ms but no more than 400 ms. We required that eye velocity immediately after the first saccade during tracking tasks not be markedly lower than the velocity preceding the SWJ, so that saccades away from targets did not represent a temporary discontinuation of tracking. Eye movement analysis was performed on recordings from one eye. The amount of time subjects were actively fixating targets was monitored (removing periods during blinks), and the SWJ count was divided by the amount of time on task to compute SWJs per second. The criteria for identifying saccades required that the acceleration threshold reach 1000 deg/sec per sec (with a peak ratio of 40%). The minimum saccade amplitude was 0.150. The end velocity threshold was 15 deg/sec and minimum saccade velocity was 15 deg/sec. Ten milliseconds were added before and after length to allow for the beginning and end of saccades, to exclude the saccade data from the pursuit data.

For the second study where subjects were asked to make voluntary SWJs, three conditions for pursuing the oscillating stimulus were used. In the first condition, we measured SWJ while subjects pursued the oscillating stimulus at the four velocities used in the prior test. In the second condition, subjects were instructed to make backward SWJ-like saccades when the target crossed the center of the hemiarc. The first saccade was to move behind the target and the second to catch up to the target. One SWJ-like pair of saccades was made for every sweep of the target across the screen for the 8- and 16-deg/sec targets. For the 24- and 32-deg/sec targets, only one SWJ-like pair of saccades was made every other sweep across the screen. We did this to keep the amount of visual tracking relatively constant across velocity conditions. We chose to keep tracking time constant rather than the number of sweeps, so that the number of saccades per second of tracking could be evaluated more accurately across velocity conditions. In the third condition, subjects were instructed to make forward SWJ-like saccades. That is, the first saccade was to move ahead of the target and the second to move back to the target.

There were two conditions for fixating the stationary and remembered target location. In the first condition, subjects fixated a central cue for 15 seconds and the central fixation point was extinguished. Subjects then continued fixating the location where the central target had been for another 15 seconds. In the second condition, subjects voluntarily made SWJ-like pairs of saccades throughout the time of task performance (15 seconds). Both subjects were very familiar with the metrics of SWJ and tried to duplicate them voluntarily as accurately as possible. For this study, we did not exclude SWJ-like movements when there was pursuit gain reduction after the first saccade in pursuit tasks, and we did not have an upper limit of saccade amplitude, because significant postsaccade slowing of pursuit and larger saccades were common when subjects attempted to make voluntary SWJs.

RESULTS

Rates of SWJ during Pursuit Tasks

Figure 1 shows samples of SWJs from a representative subject during ramp and oscillating conditions. Figure 2 shows SWJ rates during pursuit. Ninety-nine percent of subjects in the high-predictability condition and 91% of subjects in the low-predictability condition made SWJs. SWJs per minute in the

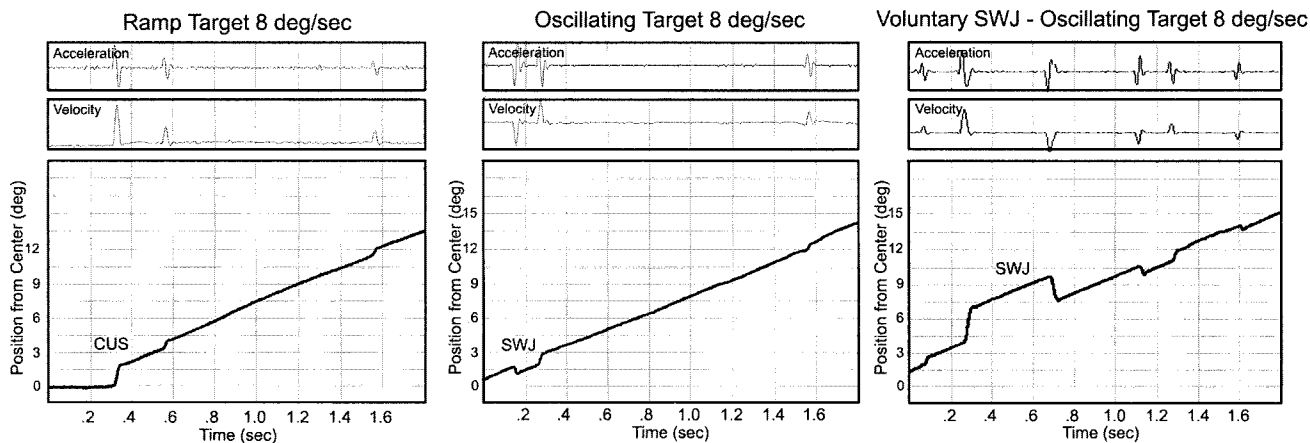


FIGURE 1. Samples of pursuit from a subject tracking targets in the ramp and oscillating conditions. Pursuit sampling was drawn from normal SWJs to the 8-deg/sec target in the ramp, or low-predictability, task (left), and the oscillating, or high-predictability, task (middle). Pursuit sampling (right) was drawn from voluntary SWJs to the 8-deg/sec target in the oscillating task. CUS, catch-up saccade.

high- and low-predictability conditions (collapsing across target velocities) were 9.34 and 2.78, respectively.

We paired the 8-, 16-, and 24-deg/sec targets in the oscillating condition with 8-, 14-, and 26-deg/sec targets in the ramp condition for statistical analysis. A main effect for a two-way (task by target speed) repeated-measures analysis of variance (ANOVA) revealed that SWJ rate significantly decreased as a function of increasing target speed in both the oscillating and ramp conditions ($F_{2,90} = 119.15; P < 0.001$). A significant interaction revealed that the higher SWJ rate in the oscillating condition was due to a notably higher SWJ rate for the slow- and medium-velocity targets ($F_{2,90} = 18.90; P < 0.001$). A one-way repeated-measures ANOVA collapsing across target velocities revealed a main effect for target type. That is, SWJ rate was significantly lower in the ramp than oscillating condition ($F_{1,90} = 82.16; P < 0.001$).

Rates of SWJ during Fixation

We collapsed target velocities in the oscillating condition and then collapsed target velocities in the ramp condition sepa-

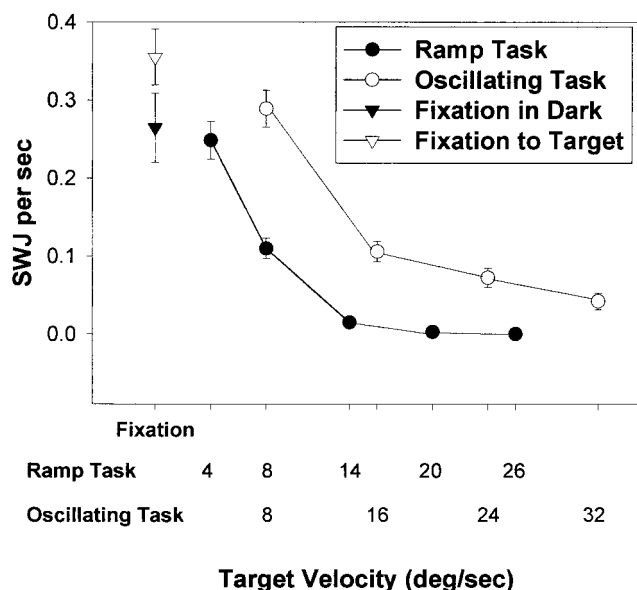


FIGURE 2. SWJ rate (\pm SE) during fixation of a stationary target, fixation of a remembered location in the dark, and pursuit of moving targets in ramp and oscillating tracking conditions.

rately. Figure 2 shows SWJ rates during both fixation conditions. We then compared SWJ rates during fixation of a visual target with rates during the oscillating condition, the ramp condition, and fixating a remembered target location in darkness using repeated-measures *t*-tests with the Bonferroni correction. Four repeated-measures *t*-tests found that SWJ rates during fixation of a visual target were significantly higher than SWJ rates in all other conditions ($t_{86} \geq 2.0; P \leq 0.05$), including fixating a remembered location in darkness ($t_{86} = 2.42; P = 0.017$). There were no significant correlations between age or sex and SWJ rate in any target condition. Figure 3 shows representative SWJs of subjects during both fixation conditions.

SWJ Amplitudes and Time between Saccades during Pursuit and Fixation

We also measured the amplitudes of SWJs in the different conditions, to test whether the benefit of having a lower SWJ rate (i.e., increase in foveation time on targets of greater inter-

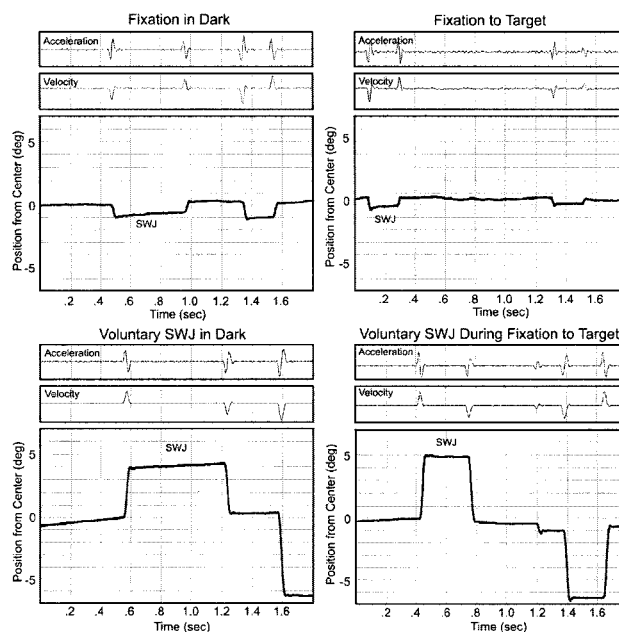


FIGURE 3. SWJs (top) and voluntary SWJs (bottom) during fixation in the dark (left) and fixation to a target (right).

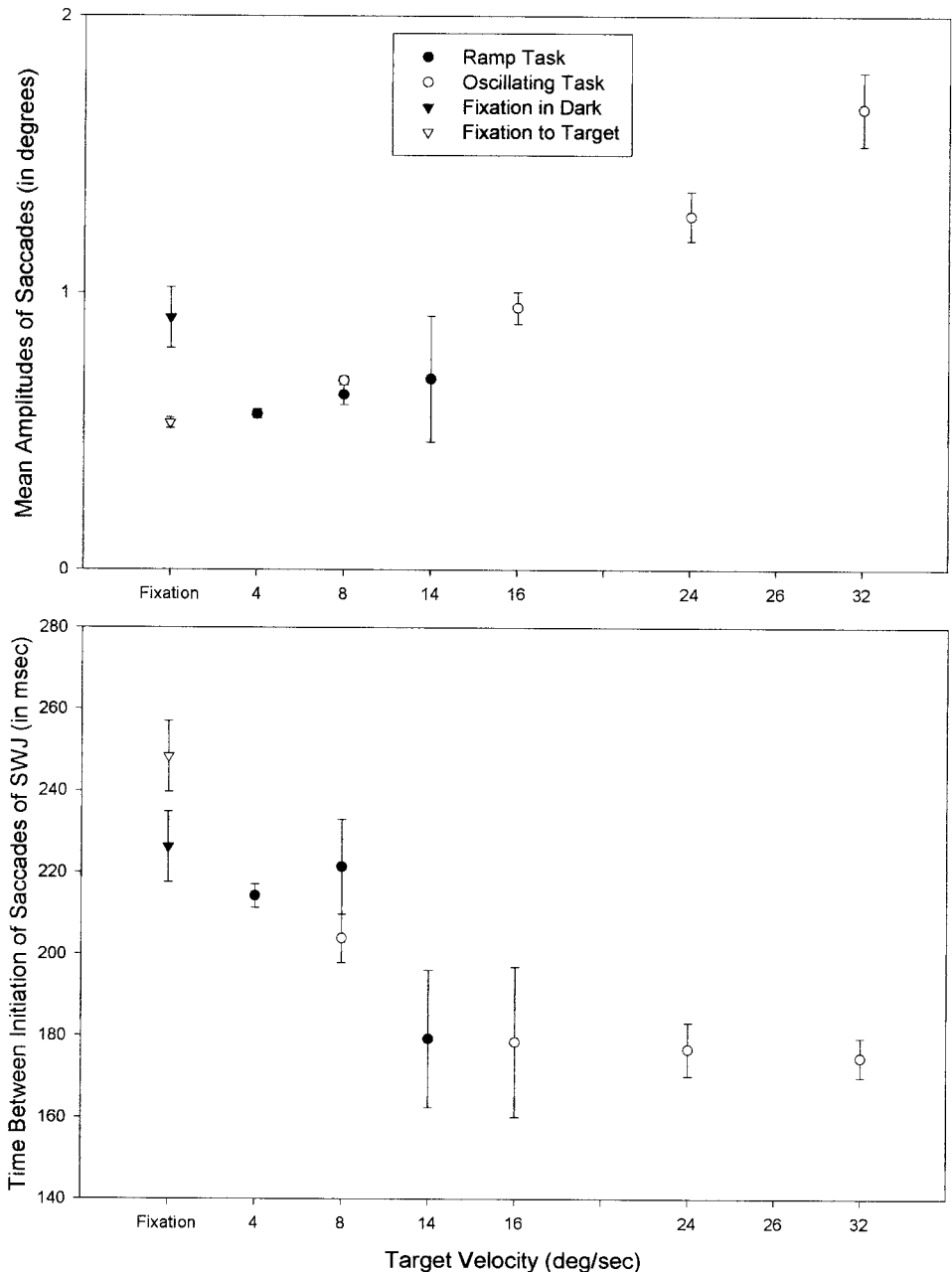


FIGURE 4. *Top:* amplitudes of saccades of SWJs during fixation of a target, fixation to a remembered target location, and at each target speed in both ramp and oscillating conditions. Because no SWJs were made in the 20- and 26-deg/sec speeds, no data points for the ramp task are shown at those speeds. *Bottom:* time between saccades comprising SWJs was measured as the time from the start of the first saccade of the SWJ and the start of the second. Because no SWJs were made in the 20- and 26-deg/sec speeds, no data points for the ramp task are shown at those speeds.

est, or having greater task demands) was countered by a longer time between saccades or larger amplitudes of saccades. Mean SWJ amplitude and mean time between the onset of the two saccades of SWJ are shown in Figure 4. A two-way repeated-measures ANOVA revealed no main effect of target speed on SWJ amplitude in the ramp task ($F_{2,135} = 0.14$, $P > 0.1$). SWJ amplitude and time between saccades did not differ significantly between oscillating and ramp conditions. Also, a two-way repeated-measures ANOVA on time between saccades revealed no main effects for target speed in either the oscillating ($F_{2,1119} = 1.15$, $P > 0.1$) or ramp condition ($F_{2,135} = 0.31$; $P > 0.1$). These findings are consistent with a benefit of increased foveation time due to reductions in SWJ frequency when tracking targets in conditions with greater task demands. However, the two-way repeated-measures ANOVA performed on SWJ amplitudes revealed a main effect for target speed in the oscillating task ($F_{2,1119} = 59.87$; $P < 0.001$), partially reducing the foveation benefits of reductions in SWJ frequency in that condition. Time between saccades did not differ signif-

icantly across the two fixation conditions, but a repeated-measures *t*-test revealed that SWJ amplitude was greater when subjects fixated a remembered target location ($t_{507} = 4.34$; $P < 0.001$).

Rates of Voluntary Versus Involuntary SWJ during Pursuit

Subjects could not voluntarily generate SWJs as they occurred naturally. Figure 1 shows samples of voluntary SWJs in one subject during pursuit. Three patterns emerged from the pursuit studies describing exactly how the metrics of voluntary SWJs differed from the metrics of involuntary SWJs. First, a one-way repeated-measures ANOVA showed that pursuit speed slowed far more after voluntary SWJs than after naturally occurring SWJs (regardless of target speed and direction; $F_{2,233} = 83.05$; $P < 0.001$). The Tukey post hoc test revealed that this effect was greater for backward than forward voluntary SWJs ($P < 0.05$). Second, a one-way repeated measures ANOVA

revealed that amplitudes of SWJs differed significantly among backward, forward, and involuntary SWJs ($F_{2,233} = 70.74$; $P < 0.001$). Specifically, the Tukey post hoc test revealed that both backward and forward voluntary SWJs were larger than for naturally occurring SWJs ($P < 0.05$). The amplitude of the first saccade of the SWJ was more than 2.5 times greater for voluntary SWJs than for naturally occurring SWJ (6.64° vs. 2.49° of visual angle). The Tukey post hoc test further revealed that forward voluntary SWJs were significantly larger than backward voluntary SWJs ($P < 0.001$). Third, a one-way repeated measures ANOVA and the Tukey post hoc test showed that the average time between saccades of SWJs was significantly longer for voluntary than for naturally occurring SWJs (ANOVA: $F_{2,233} = 21.10$; $P < 0.001$; Tukey test: $P < 0.001$). There were no statistical differences in intersaccade intervals between forward and backward voluntary SWJ.

Rates of Voluntary Versus Involuntary SWJs during Fixation

Figure 3 shows samples of voluntary SWJs in one subject during fixation of a target and of a remembered target location. For the fixation tasks, we collapsed data across voluntary SWJs (forward and backward) and across fixation conditions (to a target and in darkness to no target). A one-way repeated-measures ANOVA on the collapsed conditions showed that during fixation tasks, amplitudes of voluntary SWJs were also significantly larger than those of naturally occurring SWJs ($F_{1,58} = 11.07$, $P = 0.002$). Furthermore, a one-way repeated-measures ANOVA revealed that times between saccades of voluntary SWJs were also significantly longer than in naturally occurring SWJs during fixation conditions ($F_{1,47} = 31.45$, $P < 0.001$).

DISCUSSION

There were three main findings in the present experiments. First, few subjects in either high- or low-predictability conditions made no SWJs. Second, increasing task demands during pursuit tasks due to lower target predictability and higher target speeds significantly and progressively lowered SWJ rate. Third, naturally occurring SWJs during pursuit tracking are significantly different from voluntary efforts by highly trained subjects to look away and then back to a target. The amplitudes of saccades and velocity of pursuit between saccades were quite different when observers attempted to make SWJs deliberately than when they occurred naturally during the visual tasks used in this study. In fact, backward voluntary saccades tended more to resemble anticipatory saccades with postsaccadic slowing of pursuit, than they did involuntary SWJs, when pre- and postsaccadic pursuit speed differences are not seen. Thus, SWJ do not appear to represent voluntary shifts in gaze but rather appear to reflect a disinhibitory process that can be regulated in part by attentional and other task demands.

The present work shows that SWJ rates during fixation and pursuit varied to a great degree as a function of current demands imposed by visual tasks, with increases in different types of task demands leading to reductions in SWJ rates. Although it is not clear that SWJs in normal subjects affect vision (because the second saccade of the SWJ brings the eye back to the target), inhibition of intrusive saccades during tracking increases the probability of having the adaptive benefit of maintaining uninterrupted foveation of targets of greatest importance. Thus, there is a potential benefit from the suppression of SWJs during conditions when greater perceptual acuity is needed. From the present findings, it is difficult to say for certain whether increasing target speed and decreasing target predictability exert an effect on SWJ frequency by increasing attentional demand. However, it is clear that increas-

ing the target speed and lowering the predictability make it difficult to pursue targets and almost certainly increases resources devoted to pursuing targets.⁵⁰

As mentioned in the introduction, the prevailing clinical view is that the first saccade in an SWJ is an involuntary act caused by a failure of inhibitory control of brain stem saccade generators, as for example might result from a temporary lapse in inhibitory control of omnipause cells over saccadic burst neurons in brain stem.¹⁴ Because direct top-down modulation on pretectal regions from the frontal eye fields,^{15,16} indirect modulation through the basal ganglia onto the SC^{13,18,19} and parietal areas 7a and LIP (responsible for oculomotor and attentional cueing) may also influence SWJ rates,³¹⁻³³ it seems likely that the variation of task demands in the present work influenced the top-down modulation of the brain stem and resulted in the systematic variation in SWJ rates shown in this study. For instance, it is possible that these task demands alter the tonic inhibitory effect of omnipause neurons on burst neurons. The cortical driving of eye movements initiated by greater task demands may alter this balance through the SC or basal ganglia, so that the omnipause neurons receive greater excitatory input, making it less likely that the burst neurons will fire. Thus, rates of SWJs observed clinically may provide one index of the functional integrity of the corticofugal control of eye movement activity.

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