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Effect of Contrast on the Active Control of a Moving Line

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Li, Li, Barbara T. Sweet, and Leland S. Stone. Effect of contrast on the active control of a moving line. *J Neurophysiol* 93: 2873–2886, 2005. First published December 22, 2004; doi:10.1152/jn.00200.2004. In many passive visual tasks, human perceptual judgments are contrast dependent. To explore whether these contrast dependencies of visual perception also affect closed-loop manual control tasks, we examined visuomotor performance as humans actively controlled a moving luminance-defined line over a range of contrasts. Four subjects were asked to use a joystick to keep a horizontal line centered on a display as its vertical position was perturbed by a sum of sinusoids under two control regimes. The total root mean square (RMS) position error decreased quasi-linearly with increasing log contrast across the tested range (mean slope across subjects: -8.0 and -7.7% per \log_2 contrast, for the two control regimes, respectively). Frequency–response (Bode) plots showed a systematic increase in open-loop gain (mean slope: 1.44 and 1.30 dB per \log_2 contrast, respectively), and decrease in phase lag with increasing contrast, which can be accounted for by a decrease in response time delay (mean slope: 32 and 40 ms per \log_2 contrast, respectively). The performance data are well fit by a Crossover Model proposed by McRuer and Krendel, which allowed us to identify both visual position and motion cues driving performance. This analysis revealed that the position and motion cues used to support manual control under both control regimes appear equally sensitive to changes in stimulus contrast. In conclusion, our data show that active control of a moving visual stimulus is as dependent on contrast as passive perception and suggest that this effect is attributed to a shared contrast sensitivity early in the visual pathway, before any specialization for motion processing.

INTRODUCTION

Research over the past decade has shown that in passive speed-matching tasks, the perceived speed of moving one-dimensional (1-D) stimuli (e.g., a sine grating or line) depends on contrast with little sign of saturation at high contrast (Hawken et al. 1994; Muller and Greenlee 1994; Stone and Thompson 1992; Thompson 1982; however, see McKee et al. 1986). In general, reducing contrast causes a reduction in perceived speed. This effect has been observed not only for 1st-order motion of luminance sine gratings, but also for 2nd-order motion of contrast-modulated noise patterns (Ledgeway and Smith 1995), self-motion through optic flow (Distler and Bühlhoff 1996), and motion-in-depth from looming (Blakemore and Snowden 1999) or binocular cues (Brooks 2001). Such perceptual effects are likely the consequence of the fact that, throughout much of the primate visual pathway, neural responses increase monotonically with increasing stimulus contrast, across a wide range of contrasts (e.g., Albrecht and Hamilton 1982; Sclar et al. 1990), making the neural disambiguation of changes in contrast from those of other signal

properties problematic (see Adelson and Bergen 1986; Heeger et al. 1996; Stone et al. 1990; Thompson et al. 1996; Watson and Ahumada 1985).

Although it has clearly been established that human speed judgments during passive psychophysical testing depend on contrast, it is less clear to what extent this contrast dependency of motion perception might impact active control tasks. It has been argued that perceptual judgments and visually controlled actions involve separate, independent visual pathways (Goodale and Milner 1992; Milner and Goodale 1995). One piece of evidence for this view, relevant to the issue of contrast, is that the smooth pursuit eye movement response to constant-velocity target motion increases only slightly (about 10%) over a narrow range of target contrast above threshold (0.3 log unit), and then saturates (Haegerstrom-Portnoy and Brown 1979). This finding suggests that a steady-state motor response during a closed-loop tracking task can be relatively insensitive to changes in contrast.

Other studies, however, have shown that visually controlled actions can exhibit performance limitations similar to those shown for perception, evidenced both in accuracy (Beutter and Stone 1998; Franz et al. 2000; Krukowski and Stone 2005; Li and Warren 2002; Smeets and Brenner 1995; Soechting et al. 2001; Zivotofsky et al. 1996) and precision (Kowler and McKee 1987; Stone and Krauzlis 2003; Watamaniuk and Heinen 1999). In particular, Snowden et al. (1998) found that, when subjects were deprived of speedometer readings in a driving simulator, they drove faster when asked to maintain forward speed as the simulated scene became foggier (lower contrast), consistent with findings from their parallel passive viewing study that subjects perceived the foggier scenes as moving more slowly.

The purpose of the current study is to investigate systematically to what extent visually guided manual control is affected by display contrast. Specifically, we used a closed-loop active control task in which subjects were asked to use a joystick to control a moving horizontal luminance-defined line whose vertical position was perturbed in a pseudorandom manner. Although this task is quite simplified, it shares some essential features with real vehicular control tasks; helicopter pilots, for instance, among other tasks, must stabilize the horizon displayed on a panel to maintain a constant attitude while facing random perturbations produced by wind. Using a similar task, Zacharias and Levison (1979) previously observed a drop in gain and an increase in time delay in the control performance for a diffused line display with reduced contrast. In our study, we systematically examined the effect of changing the line

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contrast on control performance [in particular on total root mean square (RMS) position error, response gain, and time delay] under two different control regimes. In the *velocity-control* condition, the joystick displacement generated a command proportional to the rate of change of line position; in the *acceleration-control* condition, the joystick displacement generated a command proportional to the rate of change of line velocity. Velocity control is commonly experienced in many modern-world situations, such as control of an automobile in which the rate of change of direction is proportional to the steering wheel displacement. Acceleration control, although less common, less intuitive and therefore more challenging, can be mastered with practice, such as control of a spacecraft (Jagacinski and Flach 2003).

In passive speed-matching tasks, one can force observers to rely exclusively on speed information to perform the task by randomizing the temporal duration and the initial position of the moving visual stimulus to make position information irrelevant (see e.g., McKee 1981). In closed-loop active control of a moving line, however, it is difficult to separate the operator's reliance on target speed from that on target position or mere motion direction. Visual feedback data of the line speed, position, or motion direction could all be used to continuously adjust the joystick to perform the task of keeping the line centered on the screen. Given that velocity control requires the operator merely to respond to the line position, whereas acceleration control requires the operator to use feedback of the line velocity for accurate closed-loop control (Jagacinski and Flach 2003), one might expect the different joystick command dynamics of the two control regimes to influence the type of visual information subjects use for the control performance and therefore possibly to modulate any contrast sensitivity as well. To quantitatively evaluate the contrast effects on subjects' sensitivity to visual speed and position information and to determine to what extent human performance in the two control regimes may be differentially affected, we fit the performance data using a Crossover Model (McRuer and Krendel 1974; McRuer et al. 1965), tailored to assess the specific visual cues used to support performance (Sweet 1999; Sweet et al. 2003). This analysis enabled us to tease apart the overall response gain into its position and velocity components, to allow a separate examination of the contrast sensitivity of each component.

METHODS

Subjects

Four staff members (two naïve as to the specific goals of the study), between the ages of 26 and 33, at the NASA Ames Research Center participated.

Stimulus generation and control

The stimulus, which consisted of a Gaussian-blurred horizontal line ($34^\circ \text{ H} \times 1.8^\circ \text{ V}$),¹ was displayed on a FlexScan F980 Eizo 19-in. monitor ($1,240 \times 1,028$ pixels, $34^\circ \times 26^\circ$) refreshing at 60 Hz. We presented the line at five positive contrast levels (2, 3, 4, 8, and 16%) with a background luminance of 22 cd/m^2 . The line contrast was defined by the Michelson contrast formula $(L_{\max} - L_{\min})/(L_{\max} +$

TABLE 1. Magnitude and frequencies of the 10 harmonically independent sinusoids in the input position perturbation u of Eq. 1

i	a_i	k_i	ω_i , Hz
1	2	5	0.021
2	2	8	0.033
3	2	13	0.054
4	2	23	0.096
5	2	37	0.154
6	2	59	0.246
7	0.2	101	0.421
8	0.2	179	0.746
9	0.2	311	1.296
10	0.2	521	2.171

L_{\min}), where L_{\max} is the luminance of the line and L_{\min} is the luminance of the background.

During a trial, the participant was asked to use a spring-restrained joystick (B&G Systems, JF3) to keep the line centered on the monitor screen as its position was perturbed by the sum of 10 harmonically independent sinusoids. The input position perturbation u had the following form as a function of time t

$$u(t) = \sum_{i=1}^{10} D \frac{a_i 2\pi k_i}{240} \sin\left(\frac{2\pi k_i}{240} t + \rho_i\right) \quad (1)$$

Table 1 lists the actual values of a , k , and resulting frequencies ($\omega = 2\pi k/240$) used for the study. D was set to a value of 0.8° and the phase offset (ρ_i) was randomly varied from $-\pi$ to π . The use of harmonically independent sum-of-sines not only made the line motion on the screen appear random, but also allowed for a frequency-based analysis of the linear component of the control response, while minimizing artifacts from nonlinearities that might produce harmonic distortion. The average speed of the uncorrected input disturbance was $2.25^\circ/\text{s}$ (peak: $8.51^\circ/\text{s}$).

Two types of joystick control regimes were tested: the joystick displacement was proportional either to the rate of change of line position (velocity control) or to the rate of change of line velocity (acceleration control). The control regimes are specified by the controlled element dynamics Y_c implemented in software by the display computer (Fig. 1)

For velocity control

$$Y_c = \frac{1}{s} \quad (2)$$

For acceleration control²

$$Y_c = \frac{1}{s(s + 0.2)} \quad (3)$$

The joystick position was sampled at 60 Hz (i.e., every frame of the display). Thus the system feedback delay was 1 frame or 16.67 ms, which is a small fraction of the total human reaction time. Joystick displacement values ranged arbitrarily from -1 to 1 , corresponding to the full backward and forward positions, respectively.

Procedure

On each trial, a stationary line appeared and began moving when the subject pulled the trigger of the joystick. The line started moving

¹ The width of the luminance-defined line without Gaussian blurring ($\sigma = 0.5^\circ$) was 1.3° . Thus, the luminance profile of the line was $1.3 + 0.5^\circ$ wide.

² Note that our acceleration control regime was not a perfect acceleration control system of $1/s^2$. We added a damping factor of $0.2s$ to reduce task difficulty.

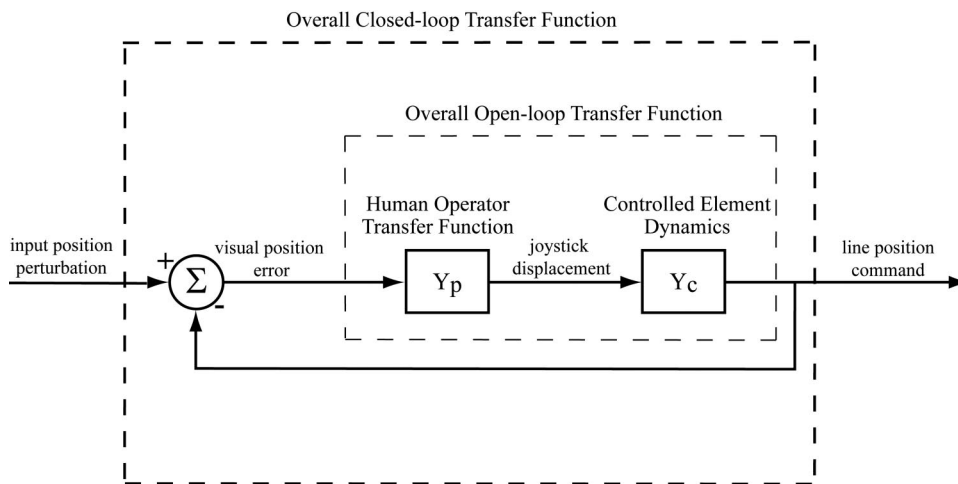


FIG. 1. Simplified block diagram of our active control task. Human operator transfer function Y_p captures the operator's control compensation, and the controlled element dynamics Y_c specifies the control regime.

according to the sum-of-sines perturbation input, and the subject's task was to move the joystick forward and backward to keep the line centered on the monitor screen. The duration of each trial was 245 s.

Six sessions, each containing 10 trials or conditions (5 contrast levels \times 2 control regimes), were run. Each subject ran one session per day for six days. Trials were blocked by control regimes and contrast levels were randomized within blocks. There was a 30-s break between trials and a 4-min break between the two blocks. To make sure subjects understood the task and became familiar with the control regimes, they received one session of practice trials before data acquisition began. An experimental session typically lasted about 1 h.

Data analysis

To investigate different aspects of the impact of contrast on performance, we used several metrics. Total performance error was measured as the RMS of the time series of recorded line position relative to the center of the screen in degrees of visual angle. We analyzed data beginning 5 s after the start of the trial to ensure that we skipped the initial transient response. To examine the operator's control response specific to the input perturbation frequencies, we performed frequency (Bode) analyses to compute both the closed-loop and open-loop describing functions from our closed-loop performance data (Fig. 1).

For the closed-loop Bode analysis, we Fourier-analyzed the input position perturbation and the line position command to obtain the relevant signal amplitudes and phases. It is possible (and in some cases desirable) to physically open the loop of a closed-loop biological control system, either by physically imposing an uncorrectable error (e.g., Jagacinski 1977; Jagacinski and Flach 2003; Pola and Wyatt 1989; Stone and Lisberger 1990) or by examining transient responses (e.g., Lisberger and Westbrook 1985). However, the problem with imposing the sustained, uncorrectable error needed to perform a steady-state Bode analysis is that the subject will likely notice this fact and will therefore change his/her strategy (e.g., either give up or work harder). Therefore a system running in such artificial open-loop conditions may not actually reflect the true open-loop transfer function of the corresponding closed-loop system. Here, we have chosen another approach; we have simply allowed the system to run in a closed loop, but have recorded the actual driving input signal throughout the trial (i.e., the imposed input partially corrected by feedback). Assuming linearity, we can derive the open-loop transfer function using the measured input and output. This approach has the advantage that we are sure that the strategy yielding the open-loop and closed-loop performance is actually the same. Thus for the open-loop Bode analysis, we Fourier-analyzed the visual position error and the

line position command to obtain the relevant signal amplitudes and phases.

In both cases, for each contrast level, we took ratios of response amplitudes and differences between the phases to compute the gain and phase lag, respectively, at each perturbation frequency, averaged across six sessions. We then used the phase of the highest contrast level (16%) as the reference and computed the relative response delay in milliseconds for the other four contrast levels. To determine the effect of contrast on performance, we conducted regression analyses on each of the above performance metrics as a function of contrast. For the slope calculations, we used data points at the lowest contrast level (2%) as the reference to calculate the percentage increase per \log_2 unit of increasing contrast. For subject RNE, we excluded his data at 2% and 3% contrast from the analysis of his RMS error for acceleration control, because he reported that he could not see the line clearly at these contrast levels and at times lost sight of the line on some of the trials, thereby causing large and uninformative RMS errors for these two conditions in the acceleration control regime.

Modeling

Our closed-loop active control task allows subjects to use the visual feedback of both line speed and position to continuously adjust the joystick to minimize the line motion and position offset on the screen. To quantitatively evaluate the contrast effects on their reliance on speed and position information in our task, we modeled the open-loop performance data using a modified McRuer Crossover Model, a linear dynamic model that describes the control compensation that humans provide for a wide variety of closed-loop manual control tasks (McRuer and Krendel 1974; McRuer et al. 1965). To illustrate the model, a simplified block diagram of the system is shown in Fig. 1.

In the model, the control compensation provided by the human operator is captured by transfer function Y_p

$$Y_p = \frac{e^{-s\tau}(sK_v + K_p)}{s^2/\omega_n^2 + 2s\xi_n/\omega_n + 1} \quad (4)$$

where τ represents the sum of the perceptual and motor delays that specify the operator's overall response time delay, K_v represents the sensitivity of the operator to stimulus speed, K_p represents the sensitivity to stimulus position offset, parameters ω_n and ξ_n represent the fixed 2nd-order response dynamics of the human operator independent of the visual stimulus, and s is the Laplace transform variable.

Model parameters were determined by a best fit to the open-loop describing function using a weighted (by SE) least-squares procedure (for details see Sweet et al. 2003). The Pearson correlation coefficients for the model estimates of subjects' average Bode plots ranged from 0.93 to 0.99 and from 0.96 to 0.9997 across subjects, for velocity and

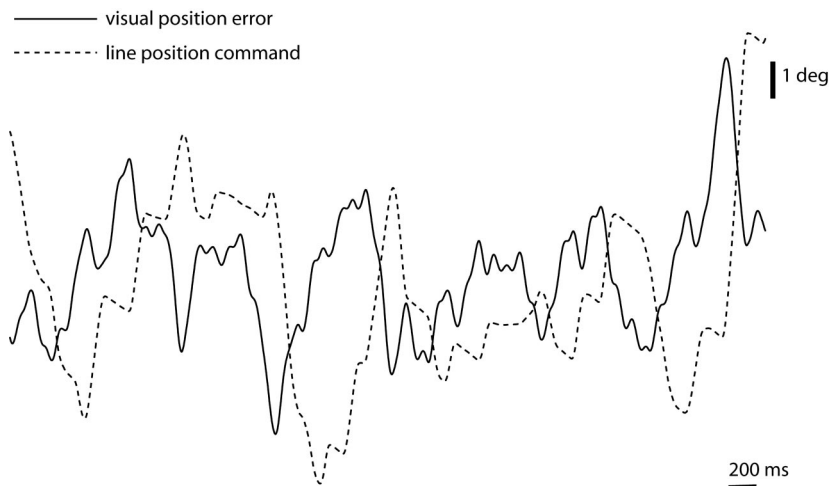


FIG. 2. Typical raw performance data of the input visual position error (solid line) and the output line position command (dashed line). Note that the output is a low-pass-filtered and delayed version of the input.

acceleration control, respectively. This indicates that between 86 and 99.94% of the variance in the individual Bode plots can be accounted for by the Crossover Model. The reduced χ^2 for the model fits to the performance data, however, ranged from 2.3 to 5.6 and from 2.8 to 5.2 across subjects, for the two control regimes respectively, indicating that, although the simple linear Crossover Model is a good fit to the data, it does not fully account for all aspects of performance. Indeed, it cannot account for any nonlinearities.

RESULTS

Overall performance

Figure 2 plots typical raw data of the visual position error and the line position command during a typical velocity control trial. In general, as expected, the joystick response is a scaled and delayed version of the input visual error signal, with a clear fall-off in the response at the highest frequencies.

The mean RMS error averaged across six sessions is plotted as a function of \log_2 contrast for each subject in Fig. 3. As expected, the RMS error for velocity control was smaller than that for acceleration control [mean: 1.70 vs. 2.68°, $t(17) = 6.89$, $P < 0.001$], consistent with the latter task's greater

difficulty. The mean RMS error averaged across subjects showed a significant linear trend with log contrast for both control regimes ($r^2 = 0.97$, $P < 0.01$ for both velocity and acceleration control). For three subjects, individual regression showed that RMS error decreased quasi-linearly with increasing log contrast across the tested range for both velocity and acceleration control ($r^2 > 0.92$, $P < 0.05$ and $r^2 > 0.87$, $P < 0.05$, respectively). For the remaining subject (AEK), the linear trend was marginally significant for velocity control, but was significant for acceleration control ($r^2 = 0.76$, $P = 0.052$ and $r^2 = 0.97$, $P < 0.01$, respectively). The mean slope (\pm SE across subjects) was -8.0 ± 1.0 and $-7.7 \pm 1.1\%$ decrease in RMS error per \log_2 contrast unit for velocity and acceleration control, respectively. There is no significant difference between these slopes [$t(3) = -1.0$, $P = 0.39$].

The RMS error measures the total performance error, both visually and nonvisually driven, and does not distinguish between errors arising from an inappropriate response amplitude from those attributed to response delay. The errors specific to the perturbation frequencies, however, are a better measure of the visually driven response specific to the moving visual stimulus, and Fourier analysis allows us to segregate response-amplitude and response-delay effects. To depict how

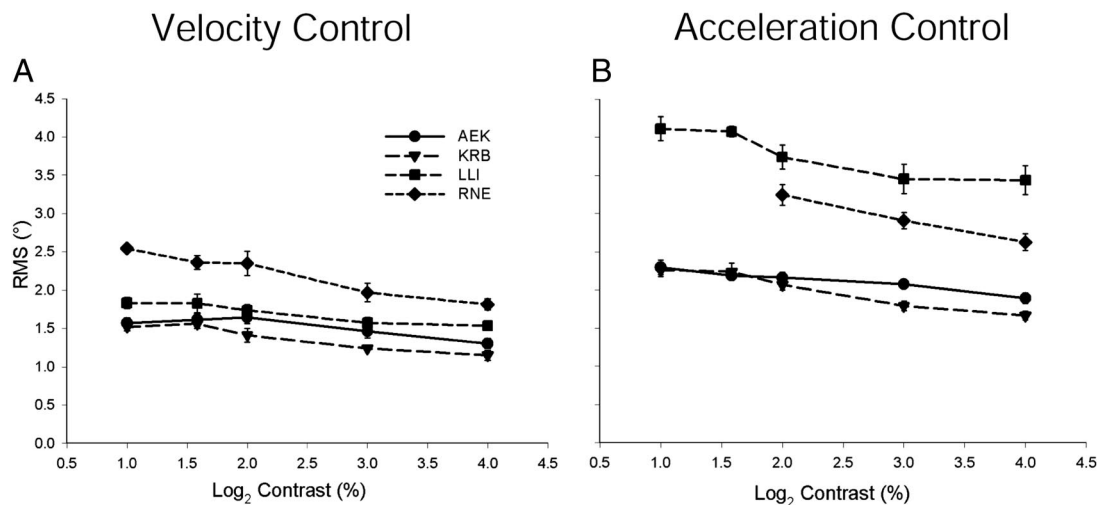


FIG. 3. Root mean square (RMS) error as a function of \log_2 contrast for velocity control (A) and acceleration control (B). Error bars represent SEs across six sessions.

Closed-loop Bode Plots

RNE

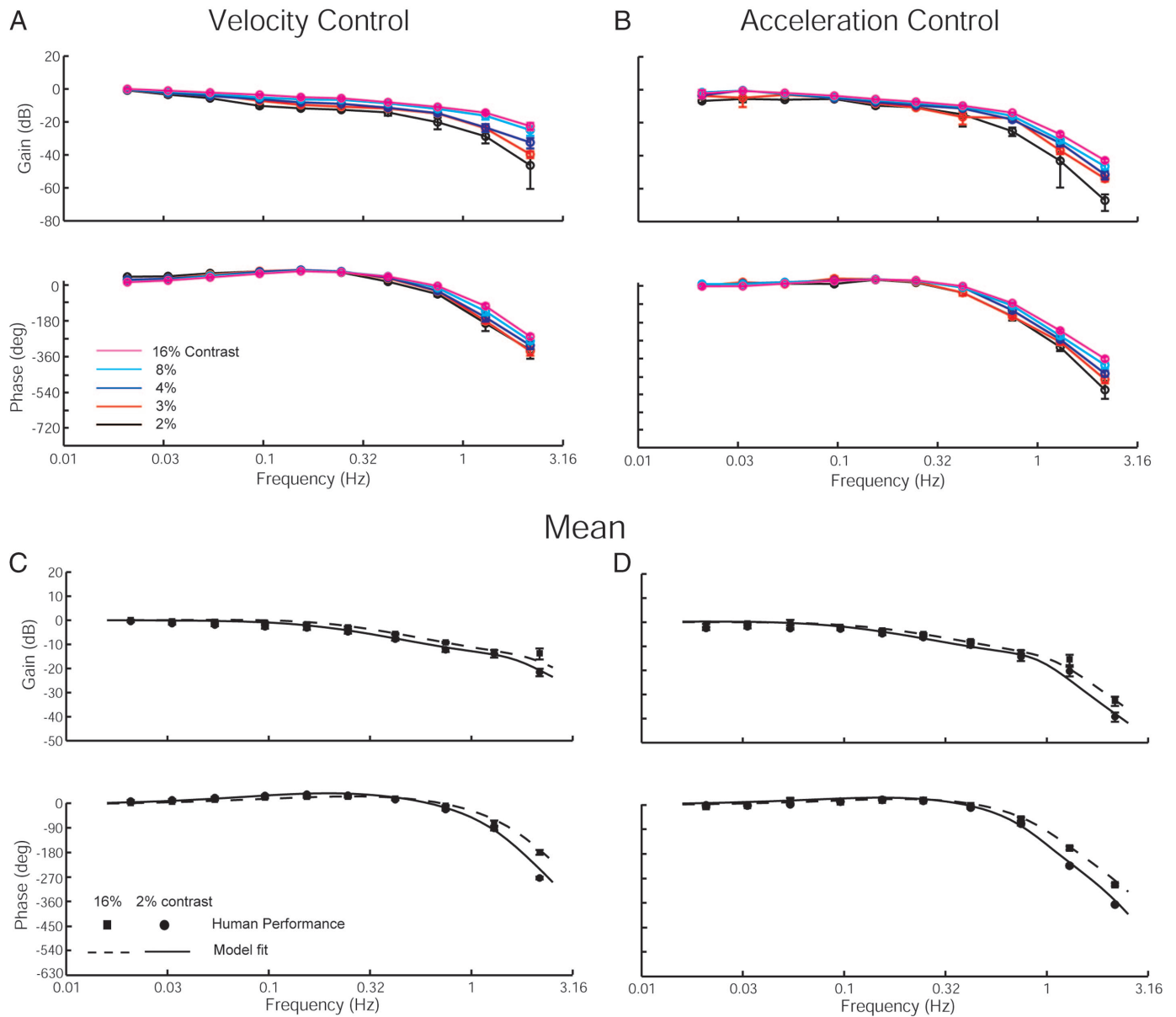


FIG. 4. Closed-loop frequency–response (Bode) plots. *Top panels*: mean gain and phase averaged over six sessions as a function of perturbation frequency for a naïve subject (RNE) for velocity control (A) and acceleration control (B). Error bars represent SEs across six sessions. *Bottom panels*: mean gain and phase averaged over four subjects as a function of perturbation frequency for velocity control (C) and acceleration control (D). Error bars represent SEs across subjects (some of them are smaller than the data symbols). Solid curves in C and D represent the best-fitting simulations of the Crossover Model, with $K_v = 0.029\%$ max/deg \times s, $K_p = 0.021\%$ max/deg, and $\tau = 329$ ms for 2% contrast in C; $K_v = 0.059\%$ max/deg \times s, $K_p = 0.031\%$ max/deg, and $\tau = 251$ ms for 16% contrast in C; $K_v = 0.030\%$ max/deg \times s, $K_p = 0.003\%$ max/deg, and $\tau = 345$ ms for 2% contrast in D; and $K_v = 0.043\%$ max/deg \times s, $K_p = 0.006\%$ max/deg, and $\tau = 267$ ms for 16% contrast in D.

the control response varies with contrast at each of the input temporal frequencies, we computed the closed-loop describing function (the ratio of the Fourier transform of the line position command to that of the input position perturbation; see Fig. 1). Figure 4, A and B, plots closed-loop gain and phase (of the command with respect to the input) as a function of perturbation temporal frequency for naïve subject RNE. The frequency–response (or Bode) plot shows that, for both

velocity and acceleration control, gain is near unity (approximately 0 dB) with little phase lag (approximately 0°) at low frequencies and shows progressive roll-off at higher frequencies. In addition, gain systematically increased and phase lag systematically decreased with increasing contrast, especially in the high-frequency range. These overall features were similar for all four subjects and the mean response is illustrated in Bode plots averaged across subjects

Open-loop Bode Plots

RNE

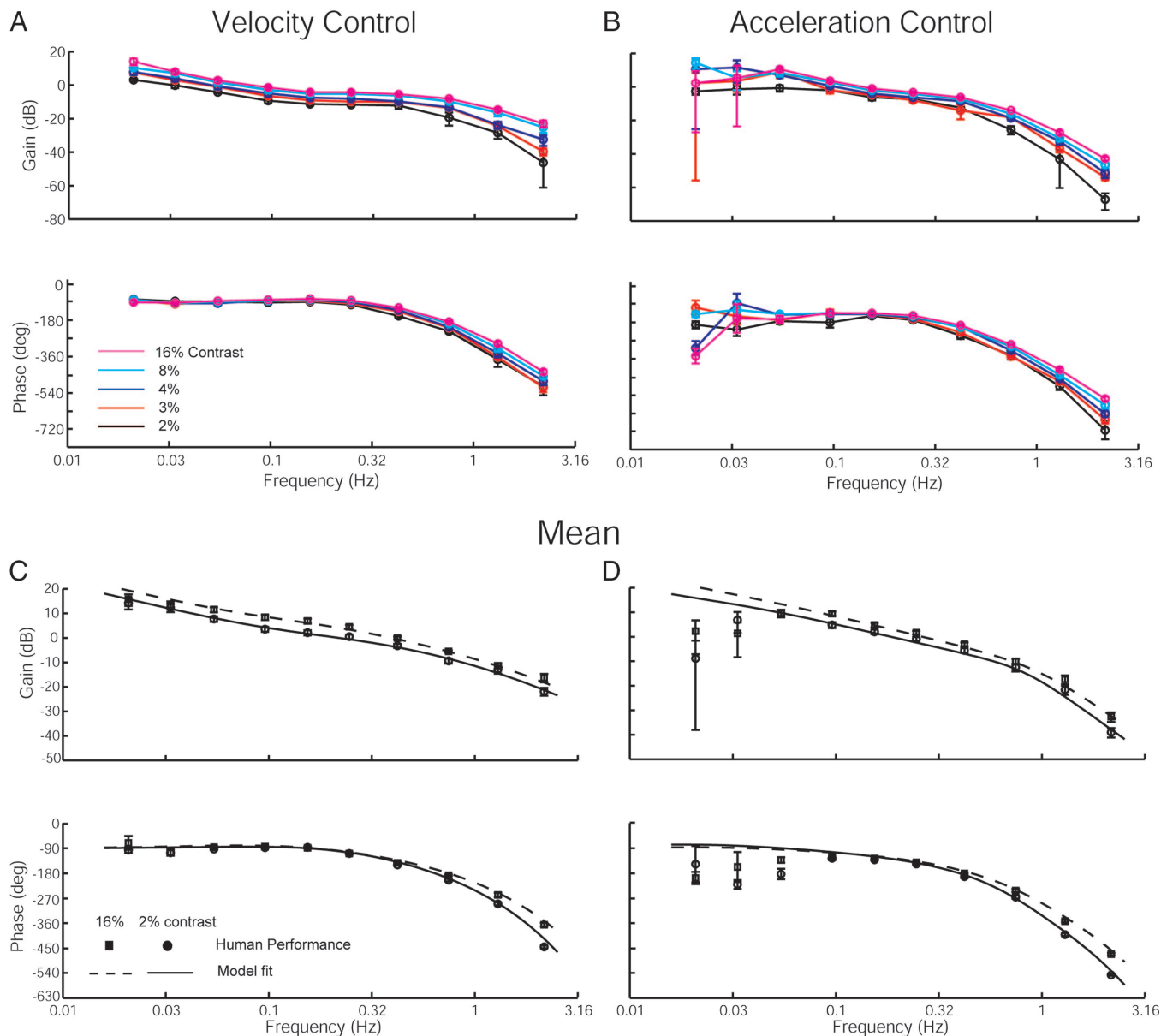


FIG. 5. Open-loop frequency–response (Bode) plots. *Top panels*: mean gain and phase averaged over six sessions as a function of perturbation frequency for a naïve subject (RNE) for velocity control (A) and acceleration control (B). Error bars represent SEs across six sessions. *Bottom panels*: mean gain and phase averaged over four subjects as a function of perturbation frequency for velocity control (C) and acceleration control (D). Error bars represent SEs across subjects (some of them are smaller than the data symbols). Solid curves in C and D represent the best-fitting simulations of the Crossover Model, with the same parameter values as in Fig. 4.

for the lowest (2%) and the highest (16%) contrast levels (Fig. 4, C and D).

Open-loop performance

The closed-loop performance of any negative feedback system is designed to be robust to large differences in the internal workings of the system (i.e., negative feedback generates nearly unity closed-loop gain over a wide range of internal gains and therefore obscures how well the internal system is

performing). To further analyze how well our subjects were performing at each of the perturbation frequencies, we also computed the overall open-loop describing function (the ratio of the Fourier transform of the line position command to that of the visual position error; see Fig. 1). Figure 5, A and B, plots the overall open-loop gain and phase as a function of frequency for naïve subject RNE. Similar to the closed-loop Bode plots, the open-loop Bode plots show overall low-pass characteristics with gain increasing systematically and phase lag decreasing

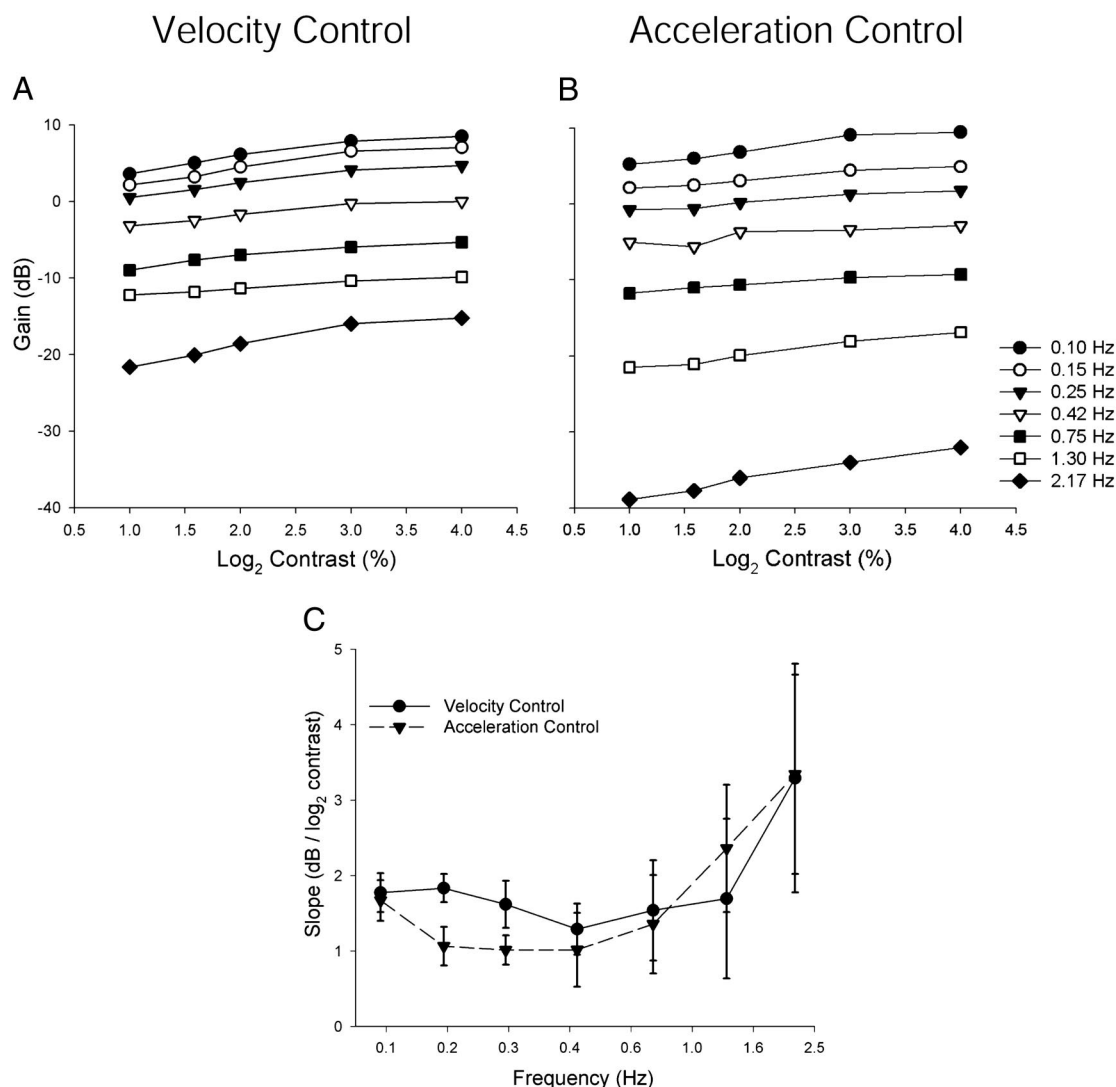


FIG. 6. Mean open-loop gain at each perturbation frequency averaged over four subjects as a function of log₂ contrast for velocity control (A) and acceleration control (B). C: mean slopes of the trends in A and B as a function of perturbation frequency. Error bars represent SEs across subjects.

systematically with increasing contrast. Unlike the closed-loop gain, the open-loop gain tends to be >1 (0 dB) and the command phase lags the input by about 90° at low frequencies, and both gain and phase roll off faster at high frequencies (e.g., Hess 1997; Jagacinski and Flach 2003), revealing a larger effect of contrast. Again, these overall features were similar for all four subjects and are illustrated in Bode plots averaged across subjects for the lowest (2%) and the highest (16%) contrast levels (Fig. 5, C and D).

To quantify the change of open-loop response gain with contrast, we plotted gain averaged across subjects as a function of log₂ contrast for each of the frequencies ≥0.1 Hz (Fig. 6, A and B). We discovered gains at the lowest three frequencies (0.02, 0.03, and 0.05 Hz) because performance measurements are noisy at these ultralow frequencies.³ Overall, the gain for velocity control was nearly double that for acceleration control [mean: -3.47 and -8.37 dB, *t*(34) = 4.93, *P* < 0.001], consistent with the latter being a more difficult task. The

overall gain averaged across frequencies showed a significant linear trend with log contrast for both control regimes (*r*² = 0.95, *P* < 0.01 and *r*² = 0.97, *P* < 0.01 for velocity and acceleration control, respectively). The overall slope (±SE across frequencies) was 1.44 ± 0.18 and 1.30 ± 0.21 dB per log₂ change in contrast for velocity and acceleration control, respectively. For all subjects, individual regression analysis showed that overall gain averaged across frequencies increased quasi-linearly with increasing log contrast across the tested range (*r*² > 0.87, *P* < 0.05 and *r*² > 0.79, *P* < 0.05, for velocity and acceleration control, respectively). The mean slope (± SE across subjects) at each frequency is plotted for each control regime in Fig. 6C. A 2 × 7 repeated-measures ANOVA on the slopes revealed that the main effect of control regime was not significant and that that of frequency was borderline [*F*(1,3) = 4.03, *P* = 0.14 and *F*(6,18) = 2.42, *P* = 0.07, respectively]. However, the interaction between control regime and frequency was highly significant [*F*(6,18) = 5.18, *P* < 0.01]. There was a tendency for both control regimes to show higher slopes (i.e., bigger contrast effects) at the lowest and highest frequencies, but velocity control's U-shaped curve

³ The measurements at these low frequencies are noisy because there are so few cycles available for Fourier analysis given the limited duration of a trial.

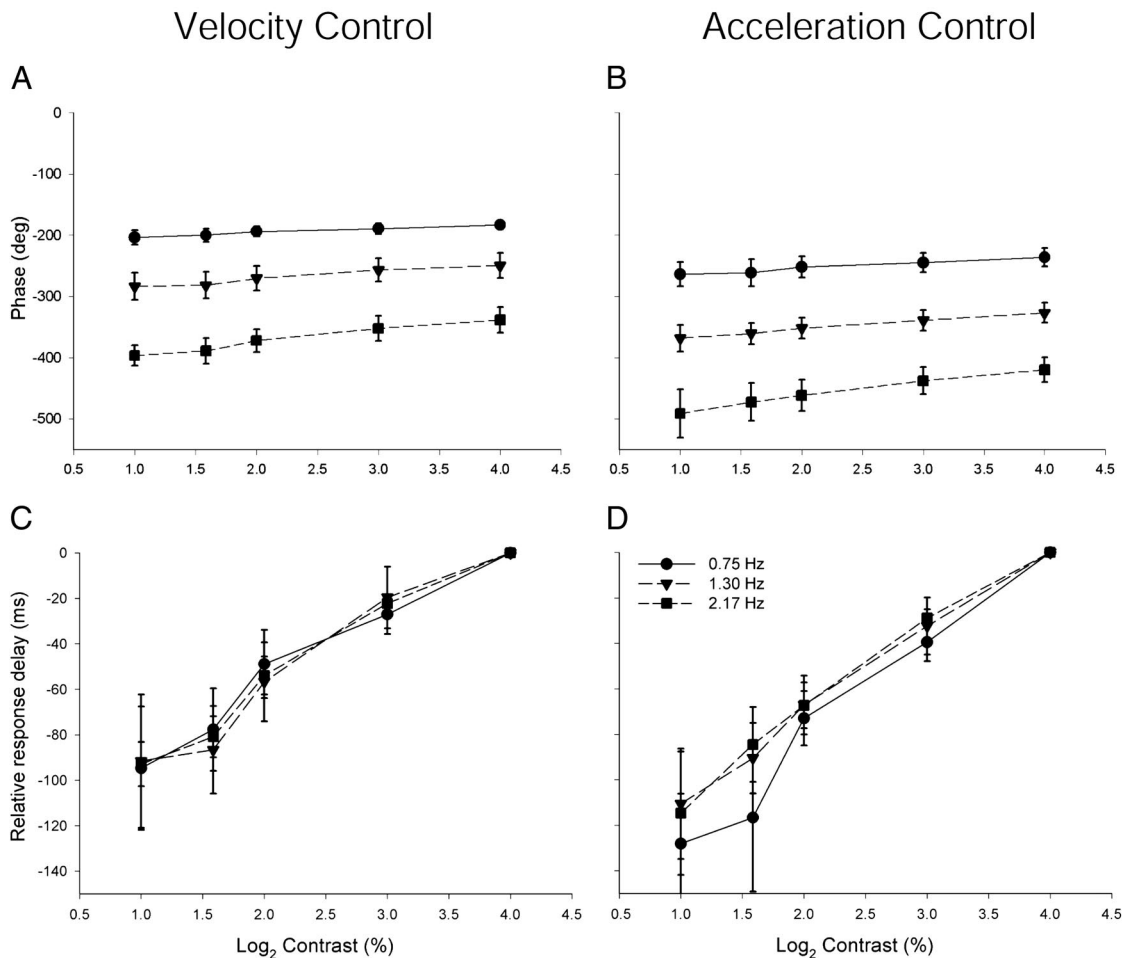


FIG. 7. Mean phase (deg) and mean relative response delay (ms) averaged over four subjects for the three highest frequencies (0.75, 1.30, and 2.17 Hz) as a function of \log_2 contrast for velocity control (A and C, respectively) and acceleration control (B and D, respectively). Error bars represent SEs across subjects.

appears to be shifted to the right with higher values than those for acceleration control in the midrange frequencies (Fig. 6C).

To analyze the effect of contrast on open-loop response phase, we first plotted mean phase as a function of \log_2 contrast (Fig. 7, A and B), averaged across subjects for the three highest perturbation frequencies (0.75, 1.30, and 2.17 Hz), chosen because the contrast effect was most reliable there (see Fig. 5). We then converted response phase to effective response time delay and plotted the mean relative delay with respect to the 16% contrast condition (Fig. 7, C and D). Although the phases at the three frequencies were quite different, as can be seen in Fig. 7, A and B, the overlap of the data in Fig. 7, C and D, shows that they nonetheless all correspond to a single response delay that varies with contrast. The overall slope (\pm SE across frequencies) was 32 ± 0.6 and 40 ± 2.7 ms per \log_2 change in contrast. There was no significant difference in these two slopes [$t(2) = -2.74$, $P = 0.11$]. Last, individual regression analysis showed that the delay increased quasi-linearly with decreasing log contrast for all subjects, across the tested contrast range, for both velocity and acceleration control ($r^2 > 0.96$, $P < 0.01$ and $r^2 > 0.97$, $P < 0.01$, respectively).

Modeling

The Crossover Model allows us to perform a quantitative evaluation of the contrast effect on human sensitivity to visual

speed and position information in our active control task. The velocity sensitivity K_v and the position sensitivity K_p capture the control characteristics subjects have in performing the task, and the time delay τ captures the overall response delay to the moving visual stimulus. Figure 8 shows the describing function of the model and illustrates how varying K_v , K_p , and τ affects overall open-loop gain and phase for the two control regimes. Specifically, increasing K_v , while keeping K_p and τ constant, causes gain in the high-frequency domain to increase (Fig. 8, A and B); increasing K_p , while keeping K_v and τ constant, causes gain in the low-frequency domain to increase (Fig. 8, C and D); and increasing τ , while keeping K_v and K_p constant, causes the phase to increase at high frequencies (Fig. 8, E and F). The solid and dashed curves in Fig. 4, C and D and Fig. 5, C and D show that the model does a good job of describing both mean closed-loop and mean open-loop performance, except for the noisy data at the three lowest frequencies under acceleration control (see footnote 3 above; see also Fig. 5D).

From the open-loop describing function, we estimated K_v , K_p , and τ for the human transfer function Y_p (Fig. 1 and Eq. 4) for all contrast and control regime conditions for each subject. We fixed ω_n and ξ_n across contrast conditions, but let them vary across control regimes. K_v , K_p , and τ were thus not directly comparable across the two control regimes, but the contrast effect (the slope as a function of contrast) was. We

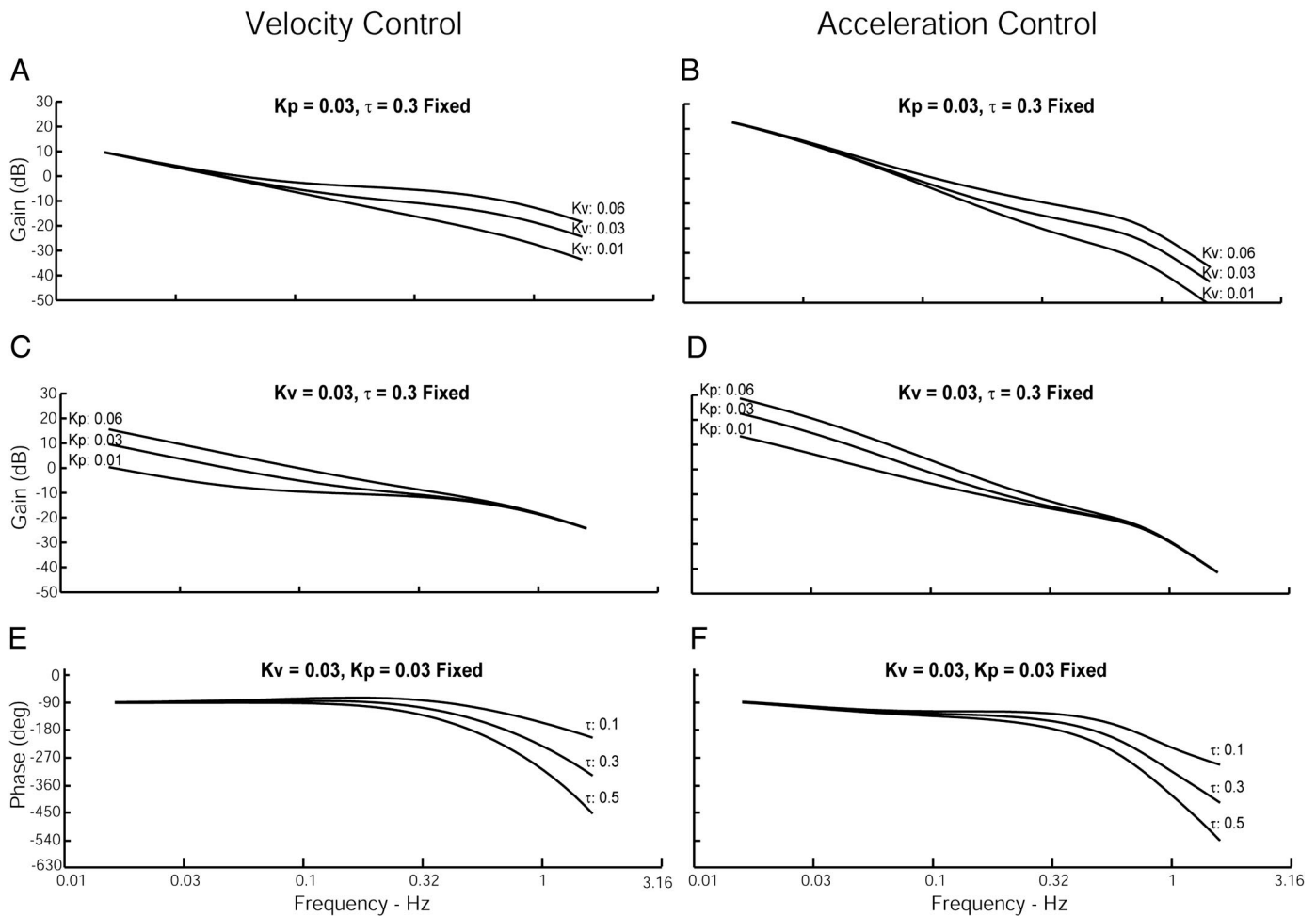


FIG. 8. Bode plots depicting effects of varying K_p , K_v , and τ on $Y_p Y_c$ of the Crossover Model under velocity control (A, C, and E, respectively) and acceleration control (B, D, and F, respectively).

graph K_v and K_p^4 as a function of contrast for each subject in log-log plots (Fig. 9). Log K_v averaged across subjects showed a significant linear trend with log contrast for both control regimes ($r^2 = 0.97$, $P < 0.01$ and $r^2 = 0.93$, $P < 0.01$ for velocity and acceleration control, respectively; Fig. 9, A and B). For three subjects, individual regression analyses showed that log K_v increased quasi-linearly with increasing log contrast for both velocity and acceleration control ($r^2 > 0.95$, $P < 0.01$ and $r^2 > 0.81$, $P < 0.05$, respectively). For subject LLI, the linear trend was significant for velocity control, but was only borderline for acceleration control ($r^2 = 0.92$, $P < 0.05$ and $r^2 = 0.72$, $P = 0.07$, respectively). The mean slope (\pm SE across subjects) was 1.53 ± 0.34 and 1.16 ± 0.40 dB change in K_v per \log_2 change in contrast. The slope for velocity control was significantly larger than that for acceleration control [$t(3) = 5.35$, $P < 0.05$], which may be related to our finding that the contrast effect on gain is higher for velocity control at the midrange frequencies (Fig. 6C).

⁴ We correlated visual position error and joystick displacement (before it goes through the control element Y_c) to estimate the model parameters for the operator transfer function Y_p . The units for position sensitivity K_p are thus a percentage of maximum joystick displacement per degree of visual angle of the line position error on the screen. For velocity sensitivity K_v , these units are then multiplied by time in seconds.

Similarly, log K_p averaged across subjects showed a significant linear trend with log contrast for both control regimes ($r^2 = 0.93$, $P < 0.01$ and $r^2 = 0.92$, $P < 0.05$ for velocity and acceleration control, respectively; Fig. 9, C and D). For subjects AEK and RNE, individual regression analyses showed that log K_p increased quasi-linearly with increasing log contrast for both velocity and acceleration control ($r^2 > 0.78$, $P < 0.05$ and $r^2 > 0.82$, $P < 0.05$, respectively). For LLI, the linear trend was significant for velocity control and nearly significant for acceleration control ($r^2 = 0.99$, $P < 0.01$ and $r^2 = 0.77$, $P = 0.0501$, respectively). For subject KRB, the linear trend was not significant for either velocity or acceleration control ($r^2 = 0.17$, $P = 0.50$ and $r^2 = 0.66$, $P = 0.09$, respectively). The mean slope (\pm SE across subjects) was 1.57 ± 0.41 and 1.51 ± 0.27 dB increase in K_p per \log_2 change in contrast. These two slopes are not significantly different [$t(3) = 0.14$, $P = 0.90$].

The model estimates of time delay τ are plotted as a function of \log_2 contrast for each subject in Fig. 10. The time delay averaged across subjects showed a significant linear trend with log contrast for both control regimes ($r^2 = 0.92$, $P < 0.01$ and $r^2 = 0.99$, $P < 0.01$ for velocity and acceleration control, respectively). For three subjects, individual regression analysis showed that τ decreased quasi-linearly with increasing \log_2 contrast across the tested range for both velocity and

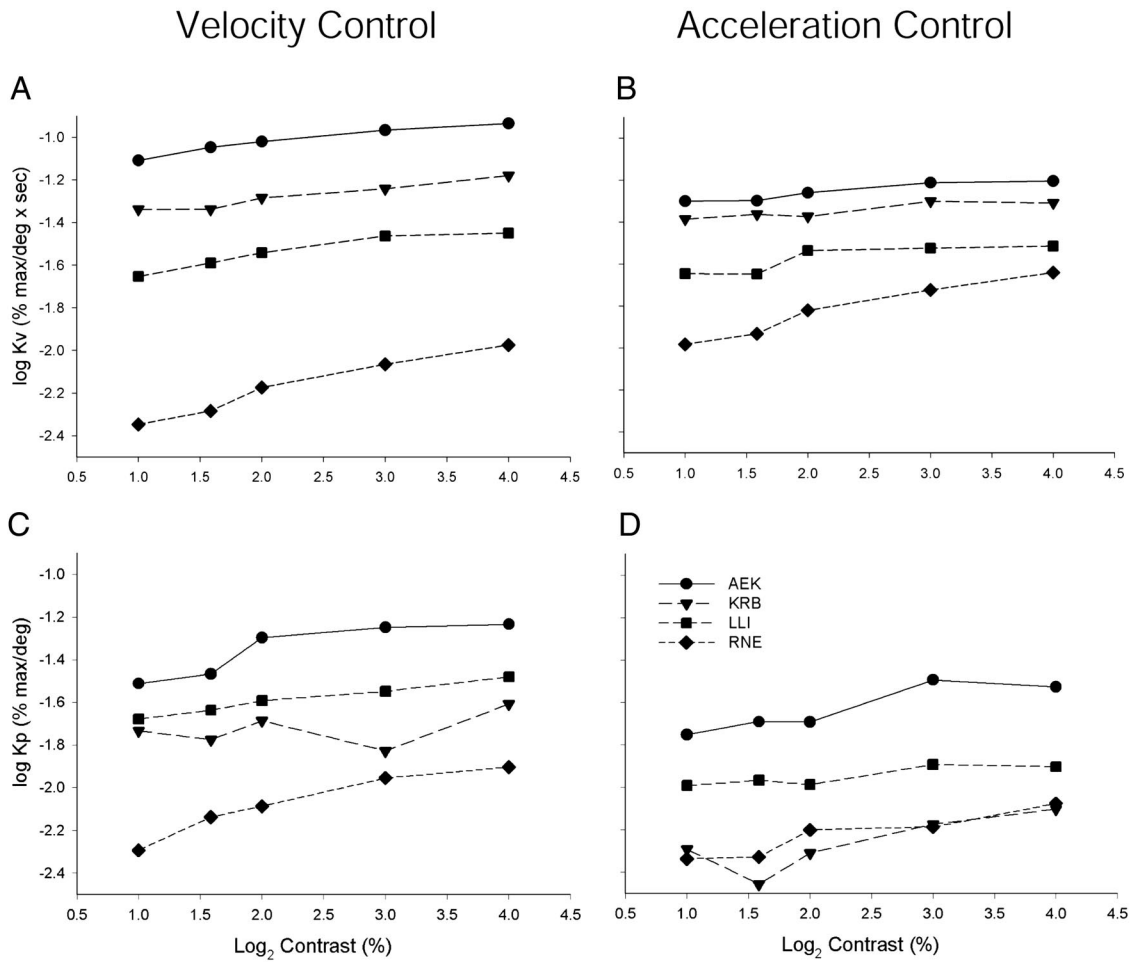


FIG. 9. Best-fitting model gain parameters for each subject as a function of \log_2 contrast. K_v for velocity control (A) and acceleration control (B); K_p for velocity control (C) and acceleration control (D).

acceleration control ($r^2 > 0.91$, $P < 0.05$ and $r^2 > 0.98$, $P < 0.01$, respectively). For subject RNE, the linear trend was borderline for velocity control, but was significant for acceleration control ($r^2 = 0.75$, $P = 0.06$ and $r^2 = 0.99$,

$P < 0.01$, respectively). The mean slope (\pm SE across subjects) was -38 ± 11.4 and -33 ± 6.0 ms per \log_2 increase in contrast. These two slopes are not significantly different [$t(3) = -0.85$, $P = 0.46$].

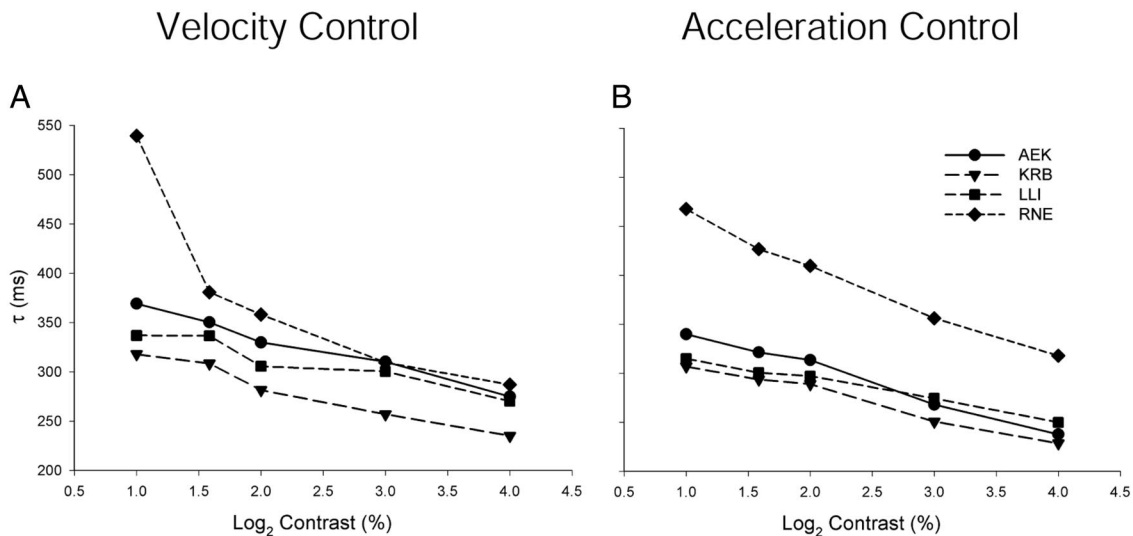


FIG. 10. Best-fitting model delay parameter for each subject as a function of \log_2 contrast. τ for velocity control (A) and acceleration control (B).

DISCUSSION

Our model-independent and model-dependent analyses both show that the active control of a moving line depends on contrast across the entire range tested (2–16%) with little sign of saturation. For an average perturbation speed of $2.25^\circ/\text{s}$ using a line of width of 1.8° , a factor of 2 increase in contrast produces an approximately 8% reduction in total RMS error, a 17% (1.4 dB) increase in internal gain, and a 35-ms decrease in reaction time, for both the velocity and acceleration control regimes. Our data also confirm that humans behave differently when interacting with velocity and acceleration control. We find, however, that the contrast effect on performance is largely independent of the control regime, suggesting that the contrast effect is largely determined by neural signals early in the visual pathway, thus producing a similar impact on both static and motion visual processing.

Reliance on position versus speed information

Humans can detect small spatial displacements and discriminate the direction of 1-D motion with performance saturating at near-threshold contrasts (Derrington and Goddard 1989; Muller and Greenlee 1994; Nakayama and Silverman 1985; Watson and Robson 1981; Wright and Johnson 1985). Our finding that active control of a moving line shows little evidence of saturation at contrasts more than an order of magnitude above threshold therefore suggests that, under both velocity and acceleration control regimes, humans do not rely merely on visual information about spatial displacement and binary 1-D motion direction to control a moving line.

Human speed perception has been shown to be dependent on contrast over a wide range of contrasts, showing little saturation (e.g., Hawken et al. 1994; Ledgeway and Smith 1995; Stone and Thompson 1992). Comparing the contrast effect in our active control task with that in passive speed-matching tasks in previous studies, we find that the magnitudes of the contrast effect are reasonably similar. For example, for a sine grating moving at $2^\circ/\text{s}$ (1.5 cpd at 3 Hz), Stone and Thompson (1992) found that the contrast effect on perceived speed is quasi-linear in log contrast with the mean slope at 9% change per \log_2 contrast (Fig. 4 in Stone and Thompson 1992). Using a sine grating moving at $1.25^\circ/\text{s}$ (4 cpd at 5 Hz) and $5^\circ/\text{s}$ (1 cpd at 5 Hz), Ledgeway and Smith (1995) found slopes of about 18% change per \log_2 contrast (Figs. 7 and 8 in Ledgeway and Smith 1995). These values are similar to those found for RMS error and open-loop gain in this study.

The human ability to detect small visual position offsets also depends on contrast over a wide range of contrasts (from 4 to 75%) with vernier thresholds increasing for decreasing contrast (Krauskopf and Farell 1991; Wehrhahn and Westheimer 1990; Westheimer et al. 1999). Assuming that the contrast effect on vernier thresholds is quasi-linear in log contrast, the mean slope of the trend is about 20% change per \log_2 contrast in both Krauskopf and Farell (1991; Fig. 4 therein) and Westheimer et al. 1999; (Table 2 therein). This slope is also in reasonable agreement with those for passive speed perception described above and those observed for our active control task. The fact that the contrast effects on position and speed discrimination have similar slopes may explain why the large difference in overall control performance observed for velocity and acceleration control was nonetheless associated with similar contrast

effects for the two control regimes. Thus manipulating contrast in an active control task, unfortunately, cannot by itself be used to disambiguate the human sensitivity to visual speed and position information when performing the task.

We therefore used a model-based analysis to address this issue. The modified McCruer Crossover Model is able to capture the characteristics of the velocity sensitivity, the position sensitivity, and the time delay in the human manual control response. The model enabled us to evaluate quantitatively the effects of contrast on the subject's reliance on speed and position information in our task. We found that both velocity and position sensitivities (K_v and K_p) increase quasi-linearly with log contrast across the tested range with slopes (1.35 and 1.54 dB per \log_2 contrast, respectively) comparable to that of the overall open-loop gain (1.37 dB per \log_2 contrast). This finding suggests that humans use both speed and position information in our active control task and that both inputs are similarly affected by contrast. Although some studies have argued that humans act simply like position servo systems when performing manual control tasks (e.g., Navas and Stark 1968), our data are consistent with previous findings that show that both visual position and motion signals are used to control steady-state smooth-pursuit eye movements (Morris and Lisberger 1987; Pola and Wyatt 1980) and pointing/pursuit hand movements (Engel and Soechting 2000; Paillard 1996; Saunders and Knill 2004). Indeed, performance in our manual control task is qualitatively consistent with models that use feedback of both visual position and velocity signals for the control of motor action (e.g., Lisberger et al. 1987; Saunders and Knill 2004). Furthermore, the observed contrast effects on RMS error, gain, and time delay are consistent with a contrast-dependent, visual, front-end nonlinearity, followed by a threshold (see next section). However, our data are silent on many other important issues that constrain manual control models, such as the role of feed-forward or other predictive mechanisms, of proprioceptive feedback, of training, and so forth. In particular, our highly constrained 1-D joystick control paradigm did not allow us to differentiate between trajectory-based and goal-based control algorithms (see Todorov and Jordan 2002).

Time delay

The model estimates of the time delay (τ) cluster in the range of 230 to 360 ms across contrasts and control regimes. These values are well within the range expected from previous studies of both the reaction time of transient responses and the time delay of steady-state responses in manual control tasks (e.g., about 250 ms in Craik and Vince 1963; about 230 ms in Engel and Soechting 2000; about 340 ms in Masson et al. 1995; about 260–340 ms in Miall 1996; about 250 ms in Navas and Stark 1968), although longer than those found in some step-response studies (about 135 ms in Carlton 1981; about 110 ms in Gibbs 1965; about 155 ms in Prablanc and Martin 1992; about 175 ms in Saunders and Knill 2004). The temporally and spatially unpredictable nature of the visual signal experienced during the closed-loop control of our pseudorandom motion stimulus (see Carlton 1981), as well as the relatively low stimulus contrast, likely contributed to the relatively long latencies observed in our study.

The contrast effect on the best-fitting time delay in the model corresponds well to that obtained from our direct analysis of the performance phase (38 vs. 32 ms per \log_2 contrast for velocity control and 33 vs. 40 ms per \log_2 contrast for acceleration control). Similarly, previous studies have reported that contrast affects reaction times for detecting both stimulus and motion onset for sinusoidal gratings (Burr et al. 1998; Harwerth and Levi 1978; Lupp et al. 1976; Mihaylova et al. 1999; Tartaglione et al. 1975). The contrast effect on simple reaction times for detecting stationary sinusoidal gratings has a mean slope increase of about 8 ms per \log_2 contrast decrease at 0.5 cpd (Fig. 2 in Mihaylova et al. 1999) and of about 5 ms per \log_2 contrast at 1 cpd (Table 3 in Tartaglione et al. 1975). The contrast effect on reaction times for detecting the motion onset of sinusoidally modulated luminance gratings has slopes ranging from about 8 to about 35 ms increase per \log_2 contrast decrease depending on observer and base speed, with smaller contrast effects as the speed approaches $10^\circ/s$ (Fig. 4 in Burr et al. 1998). The latter study also found that reaction time appears pseudolinearly related to perceived speed (i.e., well fit by Pieron's formula with a mean exponent of 1.05; see their Table 1), consistent with the view that perceived speed is computed at an early stage in a process that partially confounds stimulus motion and contrast. This finding suggests that reaction time is largely determined by a minimum critical apparent displacement (more specifically, the integral of perceived speed over time), acting as a threshold. Furthermore, if perceived target speed rather than actual target speed provides a component of the open-loop drive, the reduction of this signal at low contrast together with the elimination of small responses by a threshold could also act to reduce overall gain and increase RMS error.

A contrast effect on reaction time has also been reported in studies of visual search (Nasanen et al. 2001) and on visuomotor control of eye movements (Haegerstrom-Portnoy and Brown 1979; Ludwig et al. 2004; Mulligan and Stevenson 2003; van Asten et al. 1988). In general, visual search time or response delay increases with decreasing contrast. Haegerstrom-Portnoy and Brown (1979) first reported that the size of the contrast effect on the latency of the initial saccadic eye movement to a ramp target is about a 50-ms decrease per \log_2 contrast. More recently, Ludwig and colleagues (2004) found that saccadic latency to stationary Gabor patches increases by nearly 40 ms per \log_2 decrease in contrast (their Table 1 using fits to data normalized for threshold differences across spatial frequency). However, using a cross-correlation analysis, Mulligan and Stevenson (2003) found that the pursuit response to a target moving randomly with a mean speed of $3.4^\circ/s$ shows an increase in response delay of only about 15 ms per \log_2 decrease in contrast.

Neurophysiological effects of contrast

The fact that previous studies have shown similar effects of contrast on both static and motion visual tasks together with our finding that significant changes in control behavior are not associated with changes in contrast sensitivity argues that the contrast-dependent effects described above are a manifestation of processing early in the visual pathway, before any specialization for motion processing. Indeed, it is well known that the activity of neurons in LGN and V1 is monotonically related to

stimulus contrast, saturating only at high contrast levels (C_{50} of 33% contrast; Table 1 in Sclar et al. 1990). Later in the visual cortical pathway, the activity of most neurons in extrastriate cortical area MT saturates at relatively low contrast (C_{50} of 7% contrast, Table 1 in Sclar et al. 1990). Although MT has been demonstrated to play a critical role in direction perception (Newsome and Pare 1988; Salzman et al. 1990, 1992), its role in speed perception is less clear (however, see Churchland and Lisberger 2001; Perrone and Thiele 2001; Priebe et al. 2003), which may explain why 1-D direction judgments saturate at low contrast (e.g., Nakayama and Silverman 1985; Watson and Robson 1981), whereas perceived speed does not (e.g., Hawken et al. 1994; Stone and Thompson 1992).

In conclusion, this study provides a quantitative description, analysis, and functional model of the effects of luminance contrast on a closed-loop manual control task. We conclude that 1) human performance in closed-loop control of a moving line is highly contrast dependent over a wide range of contrasts, showing an approximately 17% decrease in internal gain for each halving of contrast; 2) this overall contrast effect is generally similar for both velocity and acceleration control, but there appear to be subtle differences in the frequency or speed dependence of this effect in the two control regimes; 3) both the modeled velocity and position sensitivities increase quasilinearly with log contrast with similar slopes, indicating that the speed and position cues used to control a moving line are similarly contrast sensitive; and 4) contrast has a dramatic effect on response delay, adding about 35 ms of delay for every halving of contrast.

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