

Changes in motion perception following oculomotor smooth pursuit adaptation

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The hypothesis that oculomotor smooth pursuit (SP) adaptation is accompanied by alterations in velocity perception was tested by assessing coherence thresholds, using random-dot kinematograms before and after the adaptation paradigm. The results showed that the sensitivity to coherent motion at 10 deg/sec (the initial target velocity during adaptation) was reduced after the SP adaptation, ending up at a level that was between those normally observed for velocities of 10 and 20 deg/sec. This is consistent with an overestimation of the velocity of the coherent motion and suggests that SP adaptation alters not only the oculomotor output, but also the perception of target velocity.

Smooth pursuit (SP) eye movements are used to keep the image of a moving visual target on the fovea. The ability to generate accurate SP relies on an estimation of target velocity. If this estimate is inaccurate, so too will be the SP output. This relationship has been demonstrated in both monkeys and humans with lesions affecting the motion processing areas of the cortex (i.e., areas MT and MST). Not only do such subjects have difficulty detecting and discriminating motion within a visual display (see, e.g., Barton, Sharpe, & Raymond, 1995; Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Newsome & Pare, 1988; Rizzo, Nawrot, & Zihl, 1995), but they also tend to produce SP responses with reduced gains and increased phase lags (see, e.g., Dursteler & Wurtz, 1988; Dursteler, Wurtz, & Newsome, 1987; Eden, Stein, Wood, & Wood, 1994; Lekwuwa & Barnes, 1996; Morrow & Sharpe, 1993). Moreover, intracortical microstimulation within these areas in monkeys influences both motion perception (Celebrini & Newsome, 1995; Salzman, Murasugi, Britten, & Newsome, 1992) and SP responses (Komatsu & Wurtz, 1989) in a predictable fashion. Thus, a clear relationship exists between the processes involved in motion perception and those concerned with accurate SP output.

Less well understood is how the perception of motion is influenced by the movement of the eyes during SP. It has been shown, for example, that target motion appears faster during visual fixation (i.e., when the eyes are stationary and the target image sweeps across the retina) than during pursuit—an effect known as the Aubert–Fleischl phenomenon (Dichgans, Wist, Diener, & Brandt, 1975). This suggests that signals carrying information related to the movement of the eyes have an influence on the motion-

processing areas of the brain (Newsome, Wurtz, & Komatsu, 1988). Indeed, the very fact that neuronal activity is modulated within areas MT and MST during SP (see, e.g., Komatsu & Wurtz, 1988), when there is supposedly very little or no retinal image motion, provides evidence in support of such a notion.

The mechanism by which motion perception is influenced by SP has been the subject of numerous behavioral and modeling studies. Yasui and Young (1975) suggested that an internal signal related to eye motion provides positive feedback to the pursuit system and, thus, is able to influence the perception of motion. Wyatt and Pola (1979) extended these findings by showing that open-loop pursuit eye movements can create the perception of apparent motion, consistent with a positive feedback mechanism. They subsequently demonstrated behaviorally and developed a quantitative model showing that this signal was influenced by both retinal and extraretinal sources of information (Pola & Wyatt, 1989).

Given that motion perception can influence SP responses and that SP responses can, in turn, have an effect on motion perception, we predicted that adaptation of the SP system to a modified input–output relation should be accompanied by changes in the perception of motion. SP adaptation can be accomplished in several ways. For example, Optican and colleagues demonstrated that a patient with ocular muscle palsy displays large increases in SP gain in his or her good eye following 7 days of viewing the world monocularly with the weak eye (Optican, Zee, & Chu, 1985). Similar changes have been observed in normal subjects following a 10–20 min period of pursuit, during which a percentage of the recorded eye motion signal is added to target motion (Carl & Gellman, 1986). This manipulation causes an increase in target speed whenever the eyes are moved; from the point of view of the subject, it is analogous to a reduction in the innervation of the eye muscles.

Using this paradigm, it has been shown that the gain of manual tracking movements performed while visually fixating is also increased following SP adaptation (van Don-

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kelaar, Fisher, & Lee, 1994; van Donkelaar, Gauthier, Blouin, & Vercher, 1997; van Donkelaar, Gauthier, Vercher, & Blouin, 1996). This suggests that at least part of the effect occurs at a level (or levels) common to both the eye and the hand motor systems. One possibility is that the adaptation is purely motor and a parametric adjustment is made to deal with the large errors in eye motion during the modification period. For example, the gain of the visual-oculomotor transformation could be increased so that a given amount of retinal image motion leads to the production of an SP response with a larger magnitude. A generalization of this change in parametric gain to other motor systems could then account for the effect observed during manual tracking movements. Another possibility is that the actual perception of target velocity is altered. Thus, after adaptation, target motion would be perceived to be greater than it was in reality. As a result, any motor output driven by target velocity would display increased gains.

In the present study, we tested the latter possibility by assessing velocity perception before and after SP adaptation. This was accomplished by measuring the threshold for perceived coherent global motion within random-dot kinematograms. These thresholds are known to vary as a U-shaped function with respect to the *actual* velocity of the coherent motion in the display (Baker, Hess, & Zihl, 1991; Newsome & Pare, 1988). In particular, motion is difficult to detect at slow (≤ 1 deg/sec) and fast (≥ 20 deg/sec) velocities but relatively easy at moderate (~ 2 – 15 deg/sec) velocities. Coherence thresholds are also sensitive to the extent of *perceived* motion in the display, as is demonstrated by the fact that they vary systematically following exposure to stimuli that induce the motion aftereffect (Raymond, 1993a, 1993b). Thus, we hypothesized that if subjects perceive velocity to be greater following the SP adaptation period, this manipulation should lead to a predictable change in the coherence threshold for the velocity that is used during the adaptation.

METHOD

Subjects

Five subjects (2 females, 3 males; 22–37 years of age) participated in these experiments after giving informed consent. Each had normal or corrected-to-normal visual acuity, and none had any ophthalmological or neurological impairments.

Apparatus and Procedure

The subject was seated comfortably in a dimly illuminated room 28.5 cm in front of a 38-cm computer monitor used for displaying the targets. Motion of the head was stabilized with a bite bar. Eye movements were monitored with an infrared corneal reflection device (IRIS Skalar) and were sampled at 70 Hz. The IRIS was calibrated at the beginning and end of the session and just before the SP adaptation procedure (see below) by having the subject make saccades alternately to targets positioned 10 deg to the left and the right of center. At no time were any large changes in the gain of the monitoring system observed.

During each session, the subject completed one of four separate conditions in a counterbalanced order. In all four conditions, a series

of pre- and posttest trials was run, consisting of either SP eye movements or measurements of coherent motion thresholds using random-dot kinematograms. In between the pre- and the posttest trials, the subject completed either 100 SP adaptation trials or, as a control, 100 trials of normal SP. In summary, the four conditions consisted of the following combinations: pre- and posttest SP eye movements with 100 trials of SP adaptation; pre- and posttest coherent threshold measurements with 100 trials of SP adaptation; pre- and posttest SP eye movements with 100 trials of the normal SP control; and pre- and posttest coherent threshold measurements with 100 trials of the normal SP control.

Smooth pursuit adaptation procedure. Each SP adaptation trial was initiated by the subject after he or she had fixated the center of the screen. The target (1 deg square) appeared at the center of the screen when the subject pressed a handheld switch. Following a variable delay (1–2 sec), the target started moving to the right at 10 deg/sec for 200 msec, then increased to 20 deg/sec and remained at this speed for a further 400 msec. Thus, target motion consisted of a double velocity step, with the change in velocity occurring at approximately the same time as the initial catch-up saccade. The subject was required to pursue the target motion as accurately as possible. At the end of each 600-msec trial, the target disappeared, and a tone sounded, indicating to the subject that he or she should make a saccade back to the starting position. Following the saccade, the subject pressed the switch to initiate the next trial. One hundred trials were completed during the adaptation period (~ 10 min).

The use of a double velocity step has recently been shown to be a simple and effective means of adapting SP output (Kahlon & Lisberger, 1996). The motion of the target in relation to the SP response is analogous to that occurring when a percentage of eye motion is added onto target motion (Carl & Gellman, 1986; van Donkelaar et al., 1994; van Donkelaar et al., 1997; van Donkelaar et al., 1996). Thus, the percept is similar for the subject. However, the latter manipulation is more difficult technically and, because of the high eye velocities and amplitudes that are eventually produced, is limited in terms of the initial target velocities that can be used.

Normal smooth pursuit control. To ensure that any effects we observed were due to the adaptation procedure and not to the fact that the subject simply moved his or her eyes for ~ 10 min, we also ran experiments in which target velocity remained at 20 deg/sec throughout the exposure period. In all other respects, however, the experiments were exactly the same as those with the SP adaptation procedure.

Pre- and posttest smooth pursuit movements. To assess the extent of adaptation, 20 pre- and posttest SP trials were completed. These were similar in every respect to the trials occurring during adaptation, except that the target moved at 10 deg/sec for 200 msec and was then blanked. This short period of target motion was used to limit the amount of retinal image motion feedback that could occur, especially during the posttest trials where such information would rapidly diminish any adaptive effects. The subject was asked to accurately follow the target and to continue for as long as possible after it disappeared. The subjects were normally able to produce about 100–200 msec of SP under these conditions. After a further 500 msec, a tone sounded, and the subject was required to look back to the center of the screen and press the switch to initiate the next trial.

Three different variables were measured during the pre- and posttest periods: (1) initial eye motion amplitude, defined as the angle through which the eye rotated during the period before the catch-up saccade or, if no such saccade occurred, before the disappearance of the target; (2) initial catch-up saccadic amplitude (when it occurred); and (3) average steady-state eye velocity, measured during the 100-msec period after the initial catch-up saccade or again, if no such saccade occurred, during the 100-msec after the disappearance of the target.

To quantify the effects of the SP adaptation procedure, the group means for the posttest scores for each of these measures were compared with those obtained in the pretest period, using repeated measures analyses of variance (ANOVAs). On the basis of previous research using similar SP adaptation procedures (Carl & Gellman, 1986; Kahlon & Lisberger, 1996), we expected the most consistent effects to be observed for the steady-state eye velocity measure only.

Pre- and posttest velocity perception. Potential changes in the perception of rightward velocity associated with SP adaptation were assessed by measuring the threshold at which coherent motion could be reliably detected within a random-dot kinematogram. During the pre- and posttest periods, the threshold was determined for an effective coherent velocity of 10 deg/sec. In addition, during the pretest period, the threshold for a 20 deg/sec effective velocity was measured. This provided a basis of comparison for the expected changes in the posttest threshold. Prior to the measurement of the pretest thresholds, a series of practice trials was completed, to acquaint the subject with the display and the procedure.

Each trial began with a fixation cross at the center of the screen, followed a random time (1–2 sec) later by a 20-deg-square display consisting of 250 small (2.5 min) white dots. With each screen refresh (70 Hz), a certain percentage of the dots were displaced either rightward or leftward. The magnitude of the displacement determined the effective velocity of the coherent motion within the display. The remaining dots were displaced in a random direction. Dots that moved off the edge of the display were replaced at the opposite end on the next screen refresh. The lifetime of each dot was 28 msec, and the display was presented for 140 msec.

At the end of each presentation, the subject made a two-alternative forced choice concerning the direction of coherent motion (i.e., rightward or leftward) within the display. Guesses were encouraged when the subject was unsure of the correct response; however, no feedback was given. Coherence was varied according to a two-up-one-down staircase procedure. For every two correct responses, the coherence level was decreased by 1.5 dB, and for every single incorrect response, the coherence level was increased by the same amount (Wattam-Bell, 1994).

The coherence threshold for rightward motion was determined by calculating the geometric mean of the percentage values for the last five of seven reversals in the staircase during trials with rightward motion. The geometric mean was used to minimize the skewing effect of any outlying data points. Although leftward and rightward motion were used with equal probability in the display, reversals related to the leftward direction did not contribute to the calculation of the thresholds. For each condition (i.e., 10 and 20 deg/sec pretest and 10 deg/sec posttest), three separate threshold values were obtained, and the individual scores for each condition represent the mean of these three.

RESULTS

Smooth Pursuit Eye Movements

Figure 1A displays examples from single trials of typical pre- and posttest SP responses produced before and after exposure to the adaptation procedure, respectively. It is clear that, following the adaptation procedure, the output of the SP system has been substantially changed. In particular, despite the fact that the retinal image motion produced by the target remained more or less the same, the subject responded with a higher level of steady-state eye velocity in the posttest trial. As was expected, the initial motion of the eye and the amplitude of the catch-up saccade did not appear to be affected to the same degree. Figure 1B shows the group means for steady-state eye ve-

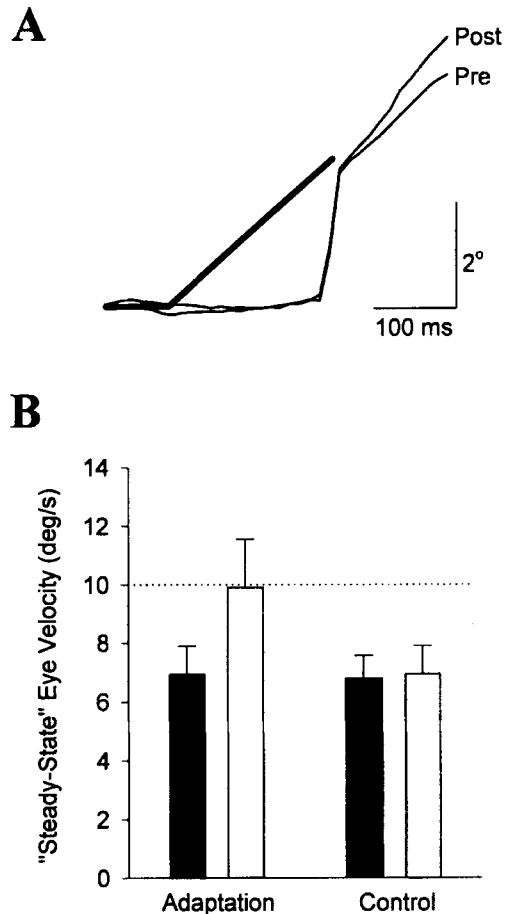


Figure 1. Effects of the smooth pursuit (SP) adaptation procedure on SP eye movements. Panel A: Examples from a single subject of typical pre- and posttest SP responses (thin traces) generated to follow the short duration target motion (thick trace). Eye velocity was substantially greater in the posttest trial (Post), as compared with the pretest trial (Pre). Note that the initial acceleration of the eye and the catch-up saccade were uninfluenced by the adaptation procedure. Panel B: Group means for steady-state SP velocity during the pretest (solid bars) and posttest (open bars) periods in the SP adaptation (left) and normal control (right) conditions. The dashed horizontal line represents target velocity. Pursuit velocity was significantly increased after exposure to the adaptation period. Error bars, average within-subjects *SD*.

locity during the pre- and posttest periods in both the adaptation and the normal control conditions. The black bars represent the pretest means, and the open bars represent the posttest means. In general, the subjects underestimated the 10 deg/sec target velocity during the steady-state period. This is consistent with previous reports of short-term open-loop SP eye movements (Becker & Fuchs, 1985). More important, it is apparent that exposure to the adaptation and to the normal control conditions had different effects on the posttest pursuit velocities. A 2×2 repeated measures ANOVA revealed highly significant effects for both the test period [pre vs. post, $F(1,4) = 34.5$,

$p = .004$] and the exposure condition [adaptation vs. normal control, $F(1,4) = 18.2, p = .013$]. There was also a significant interaction between these two factors [$F(1,4) = 48.3, p = .002$], demonstrating that the changes in the posttest scores were much more pronounced in the adaptation condition than in the normal control condition. By contrast, no significant main effects or interactions were obtained when the amplitude of the initial motion of the eye [test period effect, $F(1,4) = 0.623, p = .474$; exposure condition effect, $F(1,4) = 3.218, p = .147$; interaction, $F(1,4) = 1.314, p = .306$] or the catch-up saccade [test period effect, $F(1,4) = 0.296, p = .615$; exposure condition effect, $F(1,4) = 2.0, p = .230$; interaction, $F(1,4) = 0.678, p = .457$] was used as the dependent variable. Taken together, these results are consistent with the idea that the SP adaptation procedure mainly affects the steady-state portion of the response, while leaving the initial motion of the eye and the subsequent catch-up saccade essentially unchanged, as has been demonstrated previously (Carl & Gellman, 1986; Kahlon & Lisberger, 1996).

In order to assess the evolution of these adapted responses, we looked at the changes that occurred in SP output during the adaptation period. Figure 2A shows the 1st, 3rd, and 10th adaptation trials from a single subject. During the 1st trial, the subject produced an eye velocity that was appropriate for the initial target velocity (i.e., 10 deg/sec). By the 3rd trial, the subject had partially compensated for the large retinal errors induced by the change in target velocity and generated a pursuit response of an intermediate magnitude (i.e., ~15 deg/sec). Finally, by the 10th trial, eye velocity had reached a level that was appropriate for the second step in target velocity (i.e., 20 deg/sec).

The values for SP gain across the entire adaptation period are shown for the same subject in Figure 2B. Gain is defined as the ratio of the average steady-state eye velocity to the initial target velocity. Thus, a value of 2 indicates that the subject had fully adjusted his or her SP output to accurately track the faster target velocity. It is apparent that there was a rapid initial change in SP gain over the first few trials, followed by a much more gradual increase during the remaining trials of the adaptation period. Regression analysis revealed that this trend in the data was best fit by a natural log power function. The smooth curve in Figure 2B shows the line of best fit represented by the equation in the lower right-hand corner of the graph. Across the 5 subjects tested, the r^2 values for this type of function ranged from .50 to .62. Furthermore, the slope term (i.e., the value divided by trial number in the equation) ranged from .56 to .65, indicating that the individual changes in SP gain followed a similar time course during the adaptation period.

Velocity Perception

Figure 3 shows the average thresholds at which rightward coherent motion could be reliably detected within the random dot display in the adaptation and normal control conditions. The black bars represent the pretest mean with

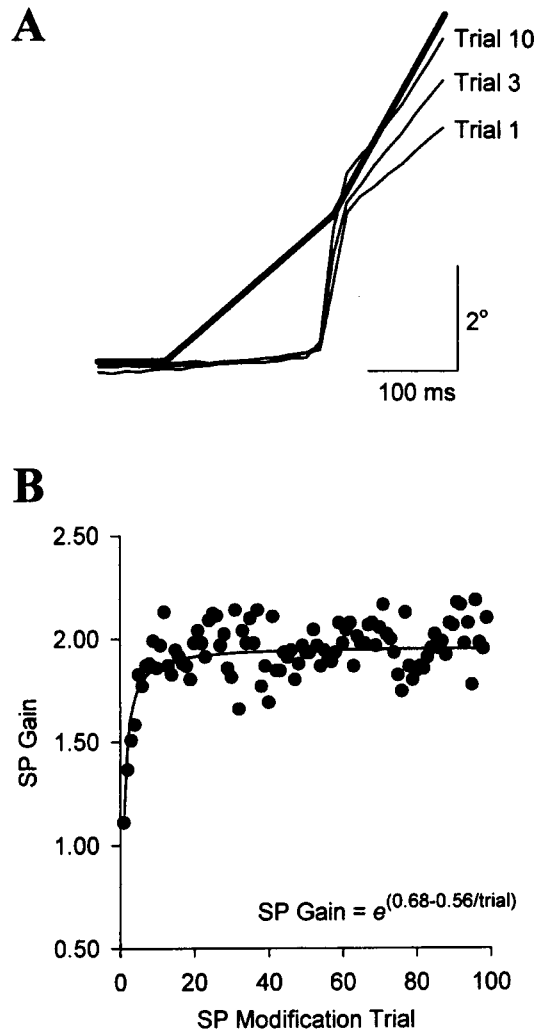


Figure 2. Changes in smooth pursuit (SP) output during the adaptation procedure. Panel A: SP responses from a single subject during the 1st, 3rd, and 10th trials (thin traces) of the SP adaptation period. Note the large increase in SP velocity in response to the second step in target velocity (thick trace). Panel B: SP gain scores calculated with respect to the initial target velocity from each trial of the adaptation period for the same subject. After an initial rapid increase over the first few trials, SP gain subsequently increased more gradually. Line of best fit is from a regression analysis represented by the equation in the lower right-hand corner of the graph.

10 deg/sec coherent motion, the open bars represent the posttest mean with 10 deg/sec coherent motion, and the gray bars represent the pretest mean with 20 deg/sec coherent motion. As was mentioned in the Method section, this latter test was used simply to provide a basis for qualitative comparison of the changes expected in motion perception following the SP adaptation procedure. Thus, the data from this test were not included in the statistical analysis. Instead, as with the eye motion data described above, a 2×2 repeated measures ANOVA was performed on the group means for the pre- and posttests thresholds

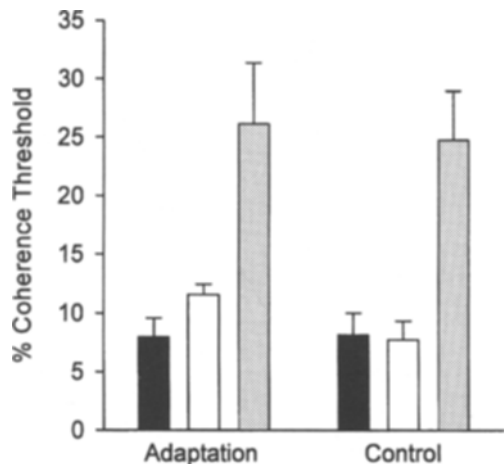


Figure 3. Group means for the threshold at which rightward motion could be reliably detected in the random-dot display. Solid bars represent pretest threshold for an effective velocity of 10 deg/sec, open bars represent the posttest threshold for the same effective velocity, and gray bars represent pretest threshold for an effective velocity of 20 deg/sec. Values on the left are from the smooth pursuit (SP) adaptation condition, and those on the right are from the SP normal control condition. Error bars, intersubject *SD*.

for the 10 deg/sec coherent motion. Statistically significant main effects were obtained for the test period [pre vs. post, $F(1,4) = 47.04$, $p = .002$] and the exposure condition [adaptation vs. normal control, $F(1,4) = 12.14$, $p = .025$]. Furthermore, the interaction between these two factors also proved to be significant [$F(1,4) = 18.91$, $p = .012$], demonstrating that the SP adaptation procedure, but not the normal control condition, causes an increase in the coherence threshold for posttest 10 deg/sec motion. Given that higher thresholds are associated with greater speeds, this suggests that the subjects overestimated target velocity under these conditions. In other words, their perception of velocity had been changed.

Comparison of Smooth Pursuit and Velocity Perception Changes

In order to more directly compare the alterations in each task, we computed the percentage change in SP steady-state velocity and perceived velocity. The former value was obtained simply by dividing the posttest means by the pretest means for each subject. For the latter measure, we interpolated where the posttest 10 deg/sec threshold fell on a straight line connecting the 10 and the 20 deg/sec pretest thresholds for each subject, then converted this value to a percentage change score. Figure 4 displays the group means obtained from these analyses. The results showed that there was a significantly larger change (*t* test, $p < .05$) in SP steady-state velocity (~50%) than in the perception of motion (~20%). This suggests that the changes in SP output can only partially be accounted for by the alterations in motion perception. The remaining difference must be due to modifications that are specific

to the process by which motion information is transformed into the pursuit response.

DISCUSSION

This study was undertaken in an attempt to gain a better understanding of the finding that manual tracking movements performed while visually fixating increased gains following SP adaptation (van Donkelaar et al., 1994; van Donkelaar et al., 1997; van Donkelaar et al., 1996). As was outlined in the introduction, this result demonstrates that at least part of the influence of the adaptation procedure occurs at a level within the central nervous system (CNS) that is common to both the eye and the hand motor systems. It has been assumed in our previous reports that this common level is related to the initial visual processing of target motion. This assumption was directly tested in the present experiments and proved to be correct. In particular, we demonstrated that the threshold at which motion could be reliably detected within a random-dot kinematogram increases after ~10 min of exposure to an SP adaptation procedure but not after a similar period of normal SP. Because we chose an effective velocity (10 deg/sec) that was near the base of the ascending limb in the U-shaped relation between coherence threshold and velocity (Baker et al., 1991; Newsome & Pare, 1988), we conclude that this result was due to a perceptual overestimation of the coherent motion within the display. Thus, velocity perception is indeed altered when the SP system is adapted. Since manual tracking movements are also driven by target velocity, an overestimation of this parameter would lead to the increased manual tracking gains that have been observed in previous studies (van Donkelaar et al., 1994; van Donkelaar et al., 1997; van Donkelaar et al., 1996).

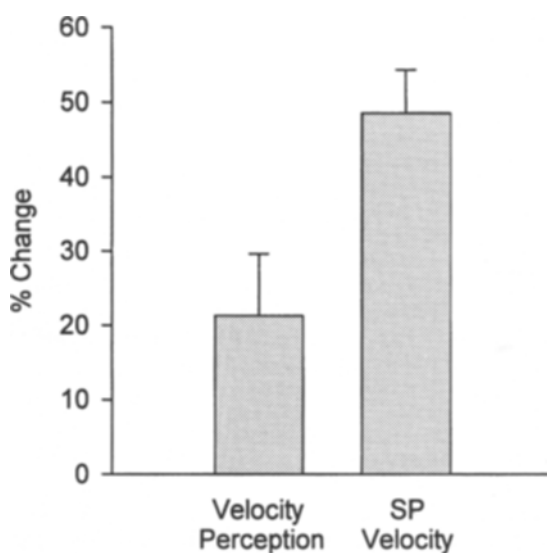


Figure 4. Group means for the percentage of change in velocity perception and smooth pursuit (SP) gain. Error bars, intersubject *SD*.

A comparison of the extents of the changes in SP gain and in visual motion sensitivity indicated that the former was influenced to a much larger extent than the latter. This suggests that the alterations in SP output cannot be completely accounted for by the change in velocity perception. Instead, additional adaptive changes must occur at levels that are beyond the initial processing of the visual motion stimulus and are more specific to the mechanisms by which this stimulus is transformed into oculomotor output. This implies that there are at least two modifiable components within the SP system: one related to the purely sensory aspects of processing visual motion, and a second concerned with the sensory to motor transformation.

Alternatively, it could be argued that the differences in the posttest changes of SP gain and velocity perception were due to the different types of stimuli that were used. In the SP task, the target was the same as that used during the adaptation period, whereas velocity perception was assessed with random-dot kinematograms. It is possible that these two types of visual stimuli are processed slightly differently by those areas of the brain that play a role in SP adaptation, thus leading to the observed discrepancy. However, this is unlikely for two reasons. First, neurophysiological experiments have shown that cells in areas MT and MST respond in a similar manner during both SP responses and visual stimulation using a single moving target (e.g., Komatsu & Wurtz, 1988; Mikami, Newsome, & Wurtz, 1986; Rodman & Albright, 1987), as well as during motion detection/discrimination tasks using a random-dot kinematogram (Salzman & Newsome, 1994). Second, L.M., an akinetopsic patient with a large lesion in the human homologue of areas MT and MST, is equally impaired on motion perception tasks that use a single target (Zihl, von Cramon, Mai, & Schmid, 1991) and those that use a kinematogram (Rizzo et al., 1995). Thus, it appears that the visual motion inherent in the two tasks used in the present experiment stimulate the motion-processing areas of the brain in a similar manner. Therefore, the incongruence observed in the posttest changes in SP gain and velocity perception must be due to real differences in the extent to which the SP adaptation procedure influences each type of task. Hence, we feel justified in concluding that the SP gain changes can be segmented into sensory and sensory-motor components.

Consistent with this segmentation is the fact that the alterations observed in previous studies for manual tracking movements following SP adaptation are similar in magnitude to those obtained in the present experiment for the sensory (i.e., velocity perception) component (van Donkelaar et al., 1994; van Donkelaar et al., 1997; van Donkelaar et al., 1996). In particular, in both cases, a change of ~20% occurred after the SP adaptation period. Thus, the perceptual overestimation of velocity can completely account for the alterations in manual tracking movements produced under similar conditions. This makes sense if one assumes that the sensory, but not the sensory-motor,

component of the SP system is common to both the eye and the hand motor systems.

The findings from the present study also have some implications for the mechanisms underlying anticipatory and/or predictive pursuit responses. Kowler and colleagues have shown that, after repeated exposure to a given visual motion condition, subjects tend to generate anticipatory or predictive pursuit responses that reflect the characteristics of that condition (see, e.g., Kowler, Martins, & Pavel, 1984; Kowler & Steinman, 1979). In this sense, it is likely that the changes we observed in SP velocity in the present study reflect anticipatory and/or predictive processes. The fact that these motoric changes were accompanied by alterations in motion perception suggests that the latter partially contribute to the development of anticipation and prediction in the pursuit system. To our knowledge, this is the first evidence to suggest that anticipatory and/or predictive pursuit responses are related to changes in the perception of motion.

An interesting remaining question, about which we can only speculate at this time, is how the process of adapting the SP system comes to alter velocity perception. One possibility is that, during the first few trials of the adaptation period, the low gain of the pursuit response leads to the overestimation of initial target velocity. This may occur through two aspects of the response. First, the retinal position and velocity errors that accumulate during the initial SP output will inform the subject that the normal magnitude of ocular muscle activation associated with the initial target velocity is no longer sufficient. One way for the CNS to interpret this is to assume that the target is moving faster than expected and to increase pursuit velocity on subsequent trials. Second, the movement of the target image away from the fovea, caused by the inappropriately low eye velocity, will lead to a situation analogous to that occurring during visual fixation, when target velocity is overestimated as a result of the Aubert-Fleischl phenomenon (Dichgans et al., 1975). Presumably, these effects would continue to reinforce the sense of increased target velocity during the remainder of the adaptation period whenever the subject generated any low-gain responses.

Neurophysiologically, there is circumstantial evidence that suggests that such a process could occur in the motion-processing areas of the cortex. In particular, Zohary and co-workers have demonstrated that cells in area MT become more sensitive to their preferred direction of motion following repeated exposure to this direction (Zohary, Celebrini, Britten, & Newsome, 1994). Not surprisingly, this increased sensitivity is accompanied by lower psychophysical thresholds for direction discrimination. Cells in MT and MST are tuned to velocity as well as to direction (Maunsell & Newsome, 1987), so it is possible that analogous modulations in a cell's response to target velocity could occur. Moreover, the extraretinal signals that provide the CNS with information related to eye motion and that appear to play a vital role in the adaptation pro-

cess (van Donkelaar et al., 1997) are known to have an influence on neuronal activity in area MST (Newsome et al., 1988).

In conclusion, the present results have provided further insight into the relationship between sensory and motor processes. More specifically, they have shown that overestimating target velocity has effects on both motor and perceptual responses. Analogous findings have recently been demonstrated for several types of visual illusion under certain conditions (e.g., Abrams & Landgraf, 1990; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Mack, Heuer, Villardi, & Chambers, 1985; Post & Welch, 1996). The interesting aspect of the present results is that the overestimation of target velocity occurred only because of the active process of generating pursuit responses during the adaptation period. This provides an example of a situation in which motor output influences the manner by which sensory information is processed.

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