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Frequency specificity in the adaptation of apparent concomitant motion

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The apparent motion of a fixated spot stimulus during head oscillations (apparent concomitant motion, ACM) was measured before and after an adaptation period during which the fixation stimulus moved in synchrony with the head. During the adaptation period, the fixation stimulus moved either in the same (*with*) or the opposite (*against*) direction as did head movement. *With* adaptation increased ACM in the direction opposite head motion, whereas *against* adaptation increased ACM in the same direction as head motion. Pre- and postadaptation measures were obtained for .25-, .5-, 1.0-, and 2.0-Hz active head movements. Each of these frequencies was used in separate sessions as the adaptation frequency. ACM changes were greatest when the test and adaptation frequencies were the same, demonstrating frequency specificity of ACM adaptation. This frequency specificity, which is similar to that of the vestibulo-ocular reflex, indicates that ACM adaptation may reflect plasticity in oculomotor systems.

The apparent stability of the visual world during head motion is referred to variously as "position constancy" (Hay & Sawyer, 1969) or "constancy of visual direction" (Wallach & Kravitz, 1965a, 1965b). This perceptual stability is often assumed to be based on a comparison of information concerning the extents of self- and image motion. Position constancy results when the perceived extent of self-motion equals the amount of image motion in the opposite direction (see Welch, 1978, for a discussion).

Small deviations from complete position constancy may be observed when a small stimulus is fixated in an otherwise dark surround during head motion. Apparent motion of a stationary stimulus during head motion has been termed *apparent concomitant motion*, or ACM (Gogel & Tietz, 1973). A technique for measuring ACM involves the presentation of a visual stimulus that moves in synchrony with the head. The amount of motion is adjustable by the observer so that the ACM is nulled and the stimulus appears stationary. The amount of physical motion required for perceptual stability indicates the degree to which a stationary stimulus would appear to move (in the opposite direction) during head movement.

Several investigators have suggested that eye movements contribute to ACM. Ronne (1923) hypothesized that the changes in perceived stability following exposure to rearranged optical conditions were the result of a modification of the vestibulo-ocular reflex (VOR). Likewise, Hay and colleagues proposed a contribution of the VOR to ACM modification (Hay, 1971; Hay & Goldsmith, 1973). Specifically, it was suggested that if compensatory eye movements are not sufficient to maintain fixation on a stimulus during head motion, the image of the stimulus should slip on the retina, thereby resulting in apparent motion in the direction opposite head movement (*against* ACM). Conversely, with excessive compensatory eye movements, the image slips in the same direction as head motion and the stimulus should appear to move in the same direction as head movement (*with* ACM).

A somewhat different mechanism by which the VOR contributes to ACM was proposed by Post and Leibowitz (1982, 1985). They suggested that the voluntary pursuit effort required to supplement a VOR gain that is too small to maintain fixation results in *against* ACM. Likewise, smooth pursuit activity initiated to oppose an inappropriately large VOR results in *with* ACM. In both cases, motion of the fixation stimulus is perceived in the direction of the pursuit effort.

Support for the hypothesis that VOR and ACM are related is provided by studies which demonstrate that both are modifiable by exposure to conditions in which the normal relationship between head and image motions is altered. VOR gain in humans is decreased with left-right reversal of the visual field (Gonshor & Melvill Jones, 1971) and increased by a period of wearing magnifying lenses (Collewijn, Martins, & Steinman, 1981a, 1981b; Gauthier & Robinson, 1975). Both of these changes in VOR gain are adaptive in that they serve to bring the VOR gain closer to that required by the new viewing conditions (for a thorough discussion, see Berthoz & Melvill Jones, 1985). Similarly, although subjects typically experience ACM during head movements when first exposed to such rearrangement conditions, the amount of ACM decreases with continued exposure (see, e.g., Hay, 1968; Wallach & Kravitz, 1965a, 1965b).

Although the similarities between VOR and ACM adaptation studies are suggestive, relatively little research has directly investigated the relationship between these two

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processes. Callan and Ebenholtz (1982) demonstrated that 20 min of exposure to optical tilt during head movement resulted in modification of the direction of the VOR. Dubois (as cited by Ebenholtz, 1986) found that similar exposure altered the direction of ACM in ways predictable from VOR modification. Post and Lott (1992) measured both ACM and VOR before and after 5 min of adaptation to a spot stimulus that moved in either the same or the opposite direction as did voluntary head oscillations of .5 or 2.0 Hz. *With* adaptation conditions decreased VOR gain and increased the tendency to see against ACM. *Against* adaptation conditions increased VOR gain and increased the tendency to see *with* ACM.

Two additional findings reported by Post and Lott (1992) may bear on the relationship between VOR and ACM. First, .5-Hz head movements resulted in a greater magnitude of *against* ACM than did 2.0-Hz oscillations. This may be related to reports that human VOR gain is constant and less than 1.0 between .1 and .5 Hz and that it increases at higher frequencies (Barr, Schultheis, & Robinson, 1976; Benson, 1970; Keller, 1978). Second, there was a tendency for adaptation to be frequency specific. That is, when subjects were adapted to .5-Hz spot motion, the magnitude of adaptation measured was greater at .5- than at 2.0-Hz test motions. Likewise, adaptation at 2.0 Hz led to stronger adaptation effects with 2.0- than with .5-Hz test motions. This frequency specificity may be related to the frequency tuning reported for VOR gain modification (Lisberger, Miles & Optican, 1983; Melvill Jones & Gonshor, 1982).

The purpose of the present paper was to assess further the frequency specificity of ACM adaptation and to investigate its possible relationship to known characteristics of the VOR. The use of only two frequencies in the Post and Lott (1992) study does not provide a basis for evaluating whether ACM depends on frequency in the way that the VOR does. As mentioned previously, VOR gain has been reported to be constant between .1 and .5 Hz, and then to increase at frequencies above .5 Hz. Therefore, it is necessary to measure ACM at frequencies both above and below .5 Hz. If VOR gain is a determinant of ACM, head movement frequencies between .1 and .5 Hz should result in a constant amount of *against* ACM. With higher frequencies of head movement, subjects should experience increasingly *with* ACM. In the present study, ACM was measured at .25, .5, 1.0, and 2.0 Hz. These values were selected to test both above and below .5 Hz, and they represent the range over which subjects can reliably generate voluntary head motions. Additionally, by using multiple frequencies, it was possible to assess the frequency tuning characteristics of the adaptation.

METHOD

Subjects

Eight adult volunteers, 20–37 years old, with normal oculomotor functions served as subjects. The subjects were either emmetropic or mildly myopic and could focus the stimulus display without spectacle correction.

Apparatus

All observations were made with the subjects seated facing a hemicylindrical projection surface (radius = 98 cm, viewing distance = 92 cm). A spot of laser light (approximately .6° in diameter) was reflected by a mirror above the subject's head onto the projection surface at eye level. An adjustable band connected the head of the subject to a potentiometer, permitting measurement of head rotation. The mirror was mounted on a galvanometer, which was driven by the signal generated by head motion and an adjustable amplifier so that motions of the spot in either the same direction as head motion or the opposite direction could be generated. The direction and gain of spot motion could be adjusted by either the experimenter or the subject with a hand-held potentiometer.

Procedure

Each subject participated in eight sessions, which were separated from each other by at least 1 day. The eight sessions represented the combination of four adaptation frequencies with two adaptation directions. During each session, measures of ACM were obtained with .25-, .5-, 1.0-, and 2.0-Hz head motions both before and after a 5-min adaptation period. Prior to each ACM measure, the experimenter adjusted the apparatus so that the spot was objectively stationary during the subject's head motion. The subjects were then instructed to open their eyes and oscillate their heads in time with a metronome, which was set to the appropriate frequency. While fixating the spot viewed against an otherwise dark surround, the subjects adjusted the potentiometer until the spot appeared stationary. Typically these settings were made within 20 sec. Subjects informed the experimenter when the spot appeared stationary, and 5-sec samples of the analogue signals of head and spot motions were digitized and stored by a microcomputer for analysis. The order of presentation of the four test frequencies was counterbalanced across subjects.

Immediately following the preadaptation measures, subjects oscillated their heads at one of the four adaptation frequencies for 5 min while attempting to fixate the spot. During this adaptation period, the spot moved either in the same direction as head motion or the opposite direction through 60% of the amplitude of head motion. Postadaptation measures were obtained immediately following this 5-min interval. The order of adaptation frequencies and directions was counterbalanced across subjects.

Data Analysis

The magnitude of ACM was computed by dividing the record of spot motion by the record of head motion obtained during the 5-sec sampling intervals. The resulting number is the percentage of the head motion that the spot moved through in order to appear stationary. Since this is a nulling measure, the sign of this value was reversed and used as the gain of ACM. ACM seen with or against head motion was assigned positive or negative values, respectively.

RESULTS

The data were first analyzed to determine the influence of frequency of head oscillation on ACM. The means of all subjects' premeasures were computed and are presented separately for each frequency of head movement in Figure 1. Between .25 and .5 Hz, ACM was similarly opposite head motion, but it decreased in magnitude with further increases in head movement frequency.

An analysis of variance (ANOVA) of the data shown in Figure 1 supported the trends apparent in the figure. Specifically, the factor of frequency was significant [$F(3,21) = 6.53, p < .01$]. Planned comparisons with the modified Bonferroni correction (Keppel, 1982) revealed no difference between the results at .25 and .5 Hz [$F(1,7) = .203, p > .5$]. However, the preadaptation measures obtained with 1.0-Hz head oscillations were sig-

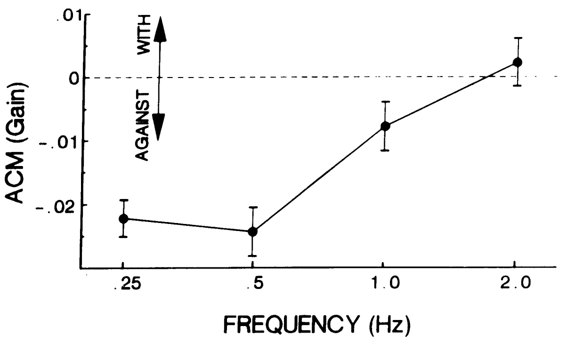

Figure 1. Preadaptation apparent concomitant motion (ACM) values expressed as the ratio of spot to head motion at each test frequency of head movement. Error bars correspond to ±1 *SEM*.

nificantly greater than those produced with .5-Hz movements [$F(1,7) = 8.89$, $p < .05$] and marginally larger than the .25-Hz results [$F(1,7) = 4.38$, $p < .1$]. With 2-Hz head movements, ACM was significantly different from both the .25- and .5-Hz measures [$F(1,7) = 9.07$, $p < .05$, and $F(1,7) = 8.08$, $p < .05$, respectively].

To investigate ACM adaptation effects, each premeasure was subtracted from its corresponding postmeasure to yield a difference score representing the strength of adaptation. These difference scores are presented separately for each frequency in Figure 2. Several trends apparent in this figure are notable. First, at each adaptation frequency, ACM is influenced by the direction of the stimulus. Following *with* adaptation, ACM is shifted against head motion, whereas *against* adaptation results in ACM in the same direction as head movement. Second, the magnitude of ACM change, as indicated by the distance separating the *with* and *against* results, increases with the frequency of adaptation. Third, these adaptation effects display frequency specificity. That is, for each of the four frequencies, ACM modification is greatest when adaptation and test frequencies are the same. The ACM adaptation is somewhat attenuated at adjacent test frequencies and smallest at the test frequency furthest from the adaptation frequency.

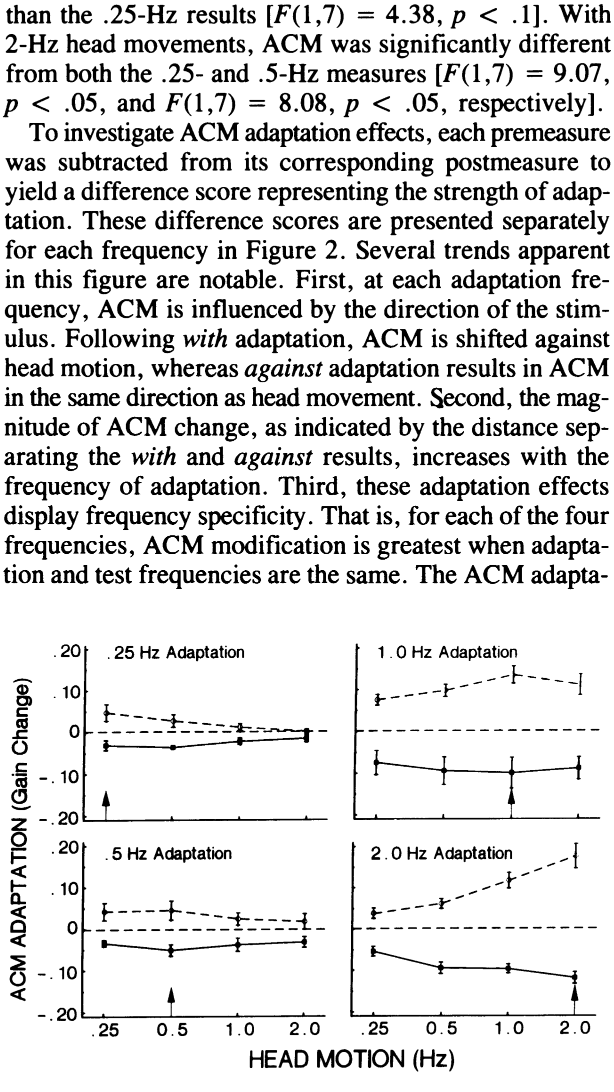

Figure 2. Mean apparent concomitant motion (ACM) difference scores (post- minus preadaptation measures) for .25-, .5-, 1.0-, and 2.0-Hz head movement frequencies (*with* adaptation = squares; *against* adaptation = circles). Arrows indicate the adaptation frequency. Error bars correspond to ±1 *SEM*.

A 4×4×2 ANOVA (adaptation frequency × test frequency × adaptation direction) was performed on the difference scores presented in Figure 2. The results of this ANOVA supported each of the previously described trends apparent in Figure 2. First, the influence of adaptation direction on ACM was highly significant [$F(1,7) = 88.4$, $p < .001$]. Second, the tendency for the magnitude of adaptation effects to increase with adaptation frequency was supported by a significant adaptation frequency × direction interaction [$F(3,21) = 40.44$, $p < .001$]. Third, the apparent frequency specificity of the adaptation effects was supported by a significant three-way interaction [$F(9,63) = 10.37$, $p < .001$]. Planned comparisons with the modified Bonferroni correction indicated that with 2.0-Hz adaptation, the differences between *with* and *against* ACM measured at the 2.0-Hz test frequency were significantly different than they were at test frequencies of 1.0, .5, and .25 Hz ($p < .01$ in each case). With 1.0 Hz-adaptation, differences were significantly greater with 1.0-Hz test motions than with 2.0-Hz ($p < .01$) and .25-Hz ($p < .05$) test motions. For the .5- and .25-Hz adaptation conditions, the effects of test frequency were not statistically significant.

DISCUSSION

The analysis of the premeasures indicated that ACM was constant and opposite head motion with .25- and .5-Hz head oscillations, and then increasingly *with* at higher frequencies. This pattern was expected on the basis of reports that VOR gain is constant and less than 1.0 between .1 and .5 Hz and increases at higher frequencies (Barr et al., 1976; Benson, 1970; Keller, 1978). When the gain of the VOR is less than 1.0, some voluntary oculomotor effort is required in the direction opposite head motion to maintain fixation. It is possible that this voluntary pursuit effort is perceived as motion of the fixated stimulus in the direction opposite head motion (Post & Leibowitz, 1985). Alternately, when VOR gain is less than 1.0, there is a tendency for the image of the fixation stimulus to slip on the retina in the direction opposite head motion, and this may be seen as object motion. With increases in frequency above .5 Hz, VOR gain increases and there is a reduction in both the fixation effort required and the amount of retinal image slip. Therefore the tendency to see opposite ACM decreases.

The analysis of the difference scores indicated that ACM was altered by 5 min of exposure to correlated head and stimulus motion at each of the four adaptation frequencies. This finding was expected on the basis of previous reports of ACM adaptation during brief intervals (e.g., Hay, 1971; Tietz & Gogel, 1978; Wallach & Kravitz, 1965b). The obtained ACM gain modification also tended to be frequency specific. This finding was anticipated on the basis of reports that VOR gain modification is frequency specific (Melvill Jones & Gonshor, 1982; Lisberger et al., 1983). Because subjects are moving their heads at one frequency during the adaptation period, the VOR gain is being modified most at that frequency and to a lesser degree at other frequencies. Accordingly, the modification of ACM similarly reflects this frequency tuning.

Unlike in previous work, in which only one or two, typically low, frequencies of head motion were examined, we employed a range of temporal frequencies and determined that the magnitude of ACM adaptation is greater at higher adaptation frequencies. The finding that the magnitude of adaptation effects is influenced by adaptation frequency may bear on the question of what neural signal underlies the adaptation. At lower frequencies, tracking of the fixation target during head motion should be nearly perfect, owing to the high gain and small phase shift of the pursuit system for predictable, low-frequency stimuli (Dallos

& Jones, 1963). Therefore, there should be little slip of the retinal image at low frequencies. At higher frequencies, however, tracking would no longer be completely compensatory, and the amount of slip should increase. The increased slip at higher frequencies might contribute to greater adaptation for two reasons. First, retinal slip has been proposed to provide the basis of VOR adaptation under conditions of correlated head and stimulus motion (Gonshor & Melvill Jones, 1976). The increased retinal slip at high frequencies of head motion might therefore produce more VOR adaptation and, consequently, greater alteration of ACM. Second, the increased retinal slip at higher frequencies might result in greater pursuit effort in an attempt to maintain fixation. Miles and Lisberger (1981) have proposed that the pursuit effort required to maintain fixation provides the neural signal that underlies VOR adaptation. Therefore the increased pursuit effort at higher frequencies might provide for more VOR adaptation and, consequently, greater alteration of ACM.

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