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Does adaptation of motion-direction detectors affect bias or sensitivity of direction judgments?

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Abstract. The question how channels tuned to different motion directions contribute to motion perception has been investigated by using motion adaptation to silence certain channels, and then measuring performance in a fine motion-discrimination task. To help constrain models of how the channels become integrated, we examined whether changes in performance stem from reduced accuracy (bias) or from reduced precision (sensitivity) in direction judgments. On a given trial, the observer first adapted to a field of dots moving coherently in a given direction (ranging $\pm 180^\circ$ from upward), then judged whether the motion of an ensuing test stimulus (ranging $\pm 3^\circ$) was left or right of reference. Bias and sensitivity of the psychometric fits were computed for each adapter direction. Relative to baseline performance, post-adaptation judgments showed significant changes in sensitivity that were tightly correlated with overall performance. Meanwhile, bias shifts were found to be weaker and less systematic. Both performance and sensitivity suffered the largest losses at $\pm 60^\circ$, with some enhancement at 180°. No similar trends were found in the domain of bias. A regression model, with precision as the sole predictor, captured 97% of the variation in performance; no gains were found in adding bias to the model. Our findings on fine motion-discrimination question the idealized notion of a pure feature detector, as the main impact of adaptation in such a system would be to bias direction judgments away from the adapted direction.

1 Introduction

The technique of psychophysical adaptation is termed the 'psychologist's microelectrode' because of its value in investigating the coding of sensory information in the human brain (Frisby 1980). The adaptation of select feature detectors in the visual system acts as a functional lesion, allowing the researcher to study the contribution of the adapted feature detectors to detection, discrimination, and visual perception in general (Clifford 2002; Regan and Beverley 1985). Adaptation is also used to study more cognitive aspects of vision, such as the mechanisms of face perception (Leopold et al 2001; Webster and MacLin 1999), and the neural substrate (He et al 1996; Humphrey and Goodale 1998) and time course (Arnold et al 2001) of visual awareness.

In particular, adaptation has been used to study motion perception. With this approach, it has been shown that the *detection* of motion is impaired most at the adapted direction (Raymond 1993) but that *discrimination* of motion direction is impaired more at directions away from the adapted direction (Phinney et al 1997). Specifically, discrimination of motion direction is most impaired at directions 60° away from the adapted direction (Hol and Treue 2001).

In the above studies, discrimination thresholds were measured by staircase methods, so the contributions of choice bias and sensitivity could not be derived. Such measures would indicate whether the adaptation process introduced directed or random noise into the behavior. This would be useful in evaluating computational models for the integration of information from different detectors.

We addressed these issues in a psychophysical study by adapting different directions ($0^\circ \pm 180^\circ$ from test direction) on different trials and observing the effects on choice bias and on sensitivity. Our results indicate that variations in performance stem mainly from change in sensitivity, rather than from bias.

2 Materials and methods

2.1 *Participants*

Observers were one of the authors and three volunteers (four in total) from the University of Houston with normal or corrected-to-normal vision who were naive as to the purpose of the study. The study was approved by the local Human Studies Committee of the University of Houston, and all participants provided written informed consent.

2.2 *Stimulus and procedure*

Observers sat at a viewing distance of 57 cm from the computer screen. The participant's head was stabilized by a chin-rest (Headspot). Software was programmed and presented with Matlab (Mathworks, Inc.) and the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997). Observers fixated on a central dot, while the stimuli (random-dot kinematograms, 87 dots per frame, 0.1 deg diameter dots, 42 cd m^{-2} luminance, background 2 cd m^{-2}, average dot lifetime 260 ms) were presented on the screen within a central viewing circle (20.5 cm diameter). A given trial typically consisted of an adapter that lasted 2 s, followed by the target stimulus, which lasted 1 s, with a 130 ms long interval in-between, during which the screen was blank. All the dots comprising the adapter or the test stimulus moved in the same direction (100% coherence). Target directions were $\pm 3°$, $\pm 2.5°$, $\pm 2°$, $\pm 1.5°$, $\pm 1°$, $\pm 0.5°$, and $\pm 0.25°$. The observer's task was to judge the direction of target motion at the end of the trial and indicate with an appropriate key-press. There were 10 conditions, characterized by adapter direction: (i) 0°, (ii) 30°, (iii) $-30°$, (iv) 60°, (v) $-60°$, (vi) 90°, (vii) $-90°$, (viii) $-180°$, (ix) 0% coherence (twinkling dots), (x) blank screen (no-adaptation baseline). Direction values are relative to upward motion, with positive values representing clockwise directions (eg 90° motion signifies motion to the right). The experiment consisted of 280 trials for each combination of adapter direction and target direction, amounting to a total of 2800 ($= 20 \times 10 \times 14$) trials per observer, ordered randomly. Inter-trial interval was 1 s. The experiment was conducted in five sessions typically spread out over 1–2 weeks. Each session contained 560 trials and took 60 min to complete for a total of 5 h per observer.

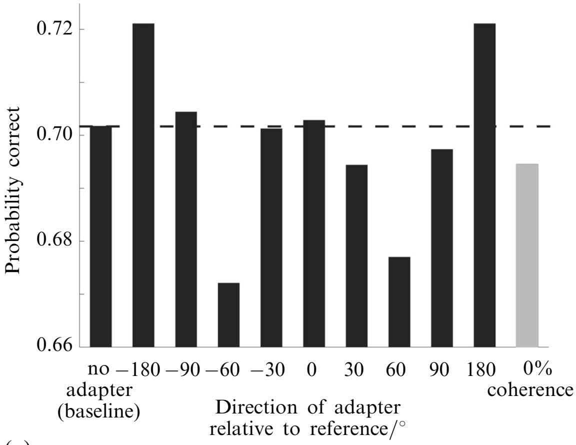
2.3 *Analysis*

Nonlinear regression, with least-squares estimation, was used to fit group data corresponding to each individual adapter condition to a cumulative Gaussian function with two parameters, μ and σ, which, respectively, represent the mean and spread of the optimal fit. The parameter μ represents the bias in direction judgment; sensitivity, or precision, and is the inverse of the spread σ. Statistics were performed with the Statistics Toolbox in Matlab. Two-tailed t-tests were used throughout.

3 Results

Figure 1a shows the plot of overall performance levels across the different adaptation conditions. The percentage of correct responses shows the largest drop when the $\pm 60°$ directions were adapted ($p = 0.003$, two-tailed). This replicates previous studies (Hol and Treue 2001), and is in line with previous claims stemming from computational models (Purushothaman and Bradley 2005). The results also show an increase in performance when the 180° direction was adapted.

Figure 1b shows the full psychometric functions (available online only, see supplementary material at http://dx.doi.org/10.1068/p6308). The group mean proportion of trials in which the observer judged the target stimulus to be drifting left of vertical is plotted as a function of actual direction of target motion. Data from each adaptation condition are fitted with a cumulative Gaussian function with two parameters, μ and σ, which, respectively, represent bias (also see figure 2a) and sensitivity (also see figure 2b).



(a)

Figure 1. Performance measures. (a) Overall percentage of correct responses (ordinate) is plotted for each adapter condition. The dashed line is the percentage correct on the no-adaptation baseline condition. The 0% coherence adapter represents motion in all directions and is shown in light gray. Directions +180° and −180° both represent downward motion, and are the same data. (b) Available online only—see http://dx.doi.org/10.1068/p6308. Group psychometric functions plotted as a function of adapter direction showing the proportion of trials where observers judged the target as moving left. Each data set is fitted with a cumulative Gaussian curve with a mean (bias) and standard deviation (sensitivity). The 60° and −60° adapter curves are red, and the 180° adapter curve is in purple. The mean and standard deviation of the cumulative Gaussian fits, which respectively correspond to bias and sensitivity^{-1}, are shown in figures 3a and 3b respectively.

Psychometric functions for the 60° and −60° conditions are shown in red, and the 180° condition is shown in purple. As figure 1b shows, the functions for these particular conditions are at the extremes in terms of their slopes, or sensitivity.

Figure 2 shows the changes in bias and sensitivity from the baseline no-adaptation condition. Since adaptation is known to cause a repulsive aftereffect, we expected judgments of the direction of the target stimulus to be biased away from the adapted direction. This is seen in figure 2a. Positive or clockwise adapter directions (30°, 60°, 90°) caused a negative bias in direction judgment, and negative adapter directions (−30°, −60°, −90°) led to a positive bias. The difference in bias between the positive and negative directions was significant ($p = 0.02$).

However, various features of the data suggest that these bias effects do not play a strong role in the overall task. In the 0% coherence control (gray bar, figure 2a), the adapter stimulates all channels equally, leading to no net motion aftereffect. When the data from this condition are used as a basis of comparison, the size of the bias shifts seen in the main conditions appears modest at best. Furthermore, the effect on sizes in the main conditions did not appear systematic. They were not monotonic with difference in direction between adapter and target, as would be expected from a linear contribution of the motion aftereffect. We were also unable to find the salient features of the performance data, such as the peak losses at ±60°, and the enhancement at 180°.

Figure 2b shows the effect of adapter direction on sensitivity of the direction judgment. In it, the standard deviation σ of the psychometric function fit, which is the reciprocal of sensitivity, is plotted. Overall, the sensitivity of direction judgments was reduced in comparison to baseline ($t_6 = 2.81$, $p = 0.03$, two-tailed). In particular, the ±60° adapters caused the greatest degradation in sensitivity, and were significantly different from the other adaptation conditions ($t_6 = 2.84$, $p = 0.03$, two-tailed). Finally, adaptation to downward motion marginally enhanced the group sensitivity of direction judgments in the opposite direction ($t_6 = 2.11$, $p = 0.08$, two-tailed). In the 0% coherence control, the effect size is on par with the main conditions.

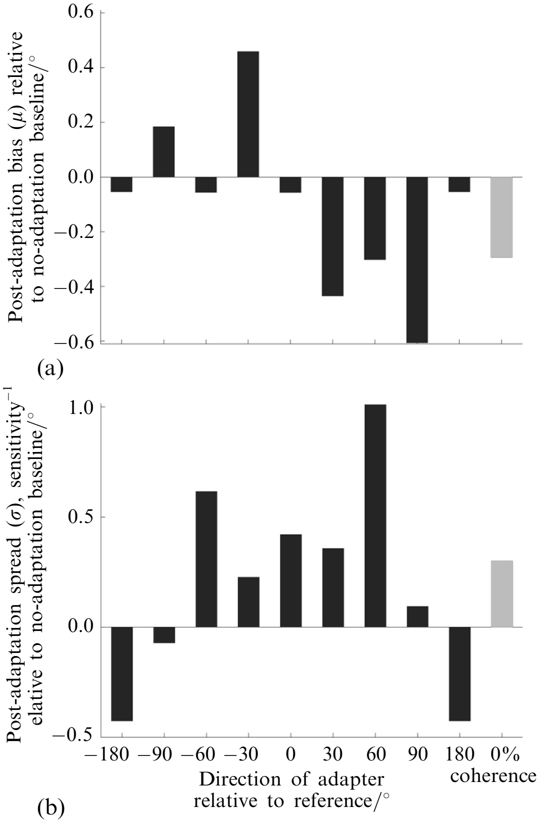


Figure 2. Parameters of performance. (a) Bias, or accuracy, of the optimal cumulative Gaussian fit as a function of adapter direction. The mean of the optimal Gaussian fit is plotted as a function of the direction of motion adaptation. All values of bias are normalized with respect to the bias in the no-adaptation baseline condition. Reference, or 0°, represents upward motion of the adapter and positive values of direction angle indicate motion clockwise of reference. (b) Sensitivity or precision of the optimal cumulative Gaussian fit as a function of adapter direction. Standard deviation, σ, following adaptation is plotted as a function of the direction of motion adaptation. Sensitivity of direction judgment is the reciprocal of the standard deviation of the fit. All values of standard deviation are normalized with respect to the standard deviation of the optimal fit of the no-adaptation baseline. In both sub-figures, directions +180° and −180° represent the same downward motion, and the same data are shown twice for clarity. The 0% coherence adapter is motion in all directions and the bias and standard deviation values on that condition are shown in gray.

As sensitivity is a measure of random noise in behavior, and since the control adapter weakly stimulates all channels, this suggests that each channel is contributing random, rather than systematic, noise.

Overall, the adaptation of motion detectors affected the sensitivity of direction judgments more than it did bias, as reflected by the mean change in each across all tested directions (σ: 0.28°; bias: 0.11°). Sensitivity of direction judgments was also more dependent on adapter direction than bias, as reflected by the relative variance of each (σ : 0.44°; bias: 0.34°). However, it is not clear that the magnitudes of bias and sensitivity can be so directly compared.

A more direct comparison of how much bias and sensitivity shifts contribute to the performance of fine motion-discrimination is contained in figure 3. Figure 3a shows a plot of the magnitude of the bias shift for each condition against task performance, measured as the percentage of correct responses. The correlation for bias is very weak ($r^2 = 0.04$, $p = 0.45$). Figure 3b is the same plot for sensitivity. This plot shows a

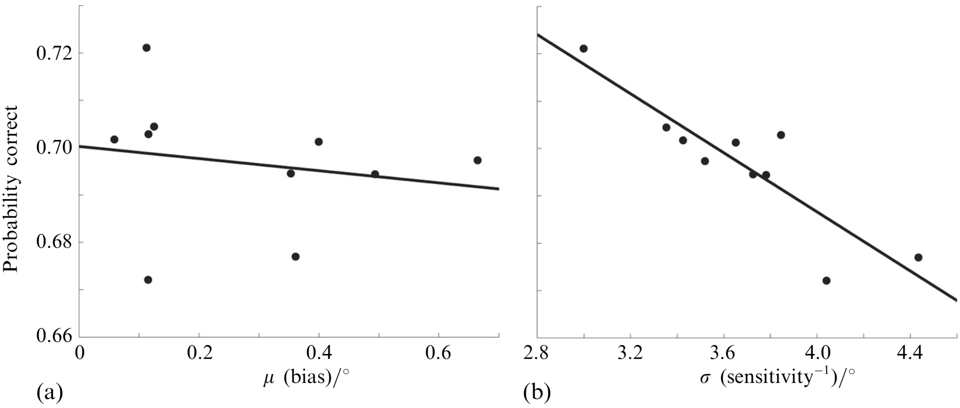


Figure 3. Linear correlation of performance with bias and sensitivity: (a) probability correct (ordinate) versus bias (abscissa) along with the optimal least-squares fit (solid black line) across all adapter conditions (including the no-adaptation baseline); (b) probability correct (ordinate) versus standard deviation (abscissa) along with the optimal least-squares fit (solid black line) across the same adapter conditions.

strong correlation ($r^2 = 0.78$, $p = 0.0007$), which is significantly stronger than that found for bias ($p < 0.0001$). In fact, a regression model with sensitivity as the sole predictor accounted for as much of the variance in performance across the different adapter conditions (97.0%) as did a model with three predictors—sensitivity, bias, and the interaction between them (96.7%).

In sum, the adaptation of selective motion directions degraded (or enhanced) the observers' ability to perform the task mainly because of its effects on sensitivity rather than bias, and increased random noise in direction judgments more than systematic noise. In addition, the sensitivity (precision) of direction judgments was found to be more variable with change in adapter direction than bias (accuracy), and different directions had differential impact on sensitivity versus bias.

4 Discussion

Using an adaptation paradigm, we psychophysically assessed the contributions of motion detectors preferring different directions of motion to the fine discrimination of motion direction about a reference (upward). Comparing the effects seen in the bias and sensitivity of judgments, we found sensitivity effects to be larger and more systematic. Sensitivity was most degraded at ±60°, and increased at 180°, in accordance with computational models and the observed performance. Most importantly, sensitivity was found to explain almost all of the variance in overall performance. Thus, we found that adaptation degraded (or enhanced) the observers' ability to perform the task mainly because of its effects on sensitivity, rather than on bias. Put another way, the adaptation of a single direction increases the random noise in direction judgments, as opposed to systematic noise. This indicates that the activity of a motion detector tuned to a particular direction does not simply bias direction judgments in favor of the tuned direction (but see below regarding mechanisms of coarse versus fine discrimination).

The performance and sensitivity data are in agreement with each other and with expectations formed from the literature. In comparison with adaptation to other directions of motion, adaptation of detectors tuned to ±60° of the reference direction reduced the sensitivity of direction judgments by the largest amount. In contrast, adaptation of motion detectors tuned to the direction opposite to the reference direction (180°) enhanced sensitivity of direction judgments. This is analogous to studies that found that adaptation to a grating oriented orthogonally to the test orientation improved orientation discrimination (Clifford 2002; Regan et al 1986).

Earlier studies have looked at the contribution of different direction detectors to motion direction discrimination (Hol and Treue 2001; Phinney et al 1997). Our study confirms and extends upon these earlier findings. Phinney et al (1997) investigated thresholds for direction discrimination of translational stereoscopic motion and found that, following adaptation in a fixed direction, discrimination thresholds were maximally elevated $20° - 30°$ away from adaptation. Unlike the present study, Phinney et al only examined the contribution of motion detectors tuned to directions within $\pm 40°$ from the reference direction, and their picture was therefore incomplete. Hol and Treue (2001) also used adaptation to examine the contribution of different motion detectors, and showed that discrimination thresholds were maximally elevated 60° away from adaptation, similar to one of our findings.

However, there are some key differences between their studies and ours. While they used staircase methods to measure thresholds, we used the method of fixed stimuli to extract full psychometric functions. This design allowed us to examine both the sensitivity and bias of direction judgments. In Hol and Treue, the adapters were transparent motion stimuli moving in diametrically opposite directions. The adapters in our study moved in a single direction, allowing us to show the individual contributions of motion detectors tuned to the diametrically opposite directions. In particular, this allowed us to test the direction 180° from the reference. Finally, two-interval direction-change judgments were used in the previous studies. Because of the built-in delay between the two stimuli, their task has a built-in memory component (Sheth and Shimojo 2001). In contrast, our task here was a single-interval absolute judgment of direction, which is more directly sensory or perceptual in nature. In this context, the replicability of the $\pm 60°$ direction finding, in spite of differences in methodology between the two studies, underscores its robustness.

It is unclear whether the conclusions we reach here for fine motion-discrimination can be extended to coarse motion-discrimination. In coarse motion-discrimination (Britten et al 1992; Newsome et al 1989), the individual (typically a monkey) distinguishes between two *opposite* directions of motion. Requirements of sensitivity in direction judgment are thus typically less in coarse discrimination than in fine discrimination; this has been offered as an explanation why, in comparison with the behavior, the most sensitive neurons in the coarse-discrimination task are *more* sensitive, but those in the fine-discrimination task are $2 - 3$ times *less* sensitive (Purushothaman and Bradley 2005). A second key difference is the fact that the most sensitive neurons in fine discrimination, unlike coarse discrimination, are not the most responsive to the target direction (0°) but rather to directions 60° away, as we have found. Supporting this assertion is another interesting fact, namely the probability correct level for the 0° adapter is not different from that obtained without adaptation (figure 1a). These differences and others between the two forms of discrimination presumably give rise to differences in neural coding scheme. In coarse discrimination, the responses of all neurons, regardless of sensitivity, are pooled (Shadlen et al 1996); in the case of fine discrimination, those of the more sensitive are believed to be assigned the greater weight (Purushothaman and Bradley 2005). On the other hand, the unbiased pooling scheme may somehow account for both kinds of discrimination.

5 Conclusion

According to models of motion discrimination, when a 'pure' direction detector adapts out, it biases discrimination judgments away from the adapted direction. Our study shows, instead, that adaptation has greater impact on sensitivity of fine judgments of motion direction, and that it corresponds more closely to performance. These findings, which show the greater impact of motion adaptation on random than systematic noise, question the idealized notion of a pure feature detector.

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