Exp Brain Res (2001) 137:254–258
DOI 10.1007/s002210000651

RESEARCH NOTE

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Motor adaptation to an optical illusion

Received: 3 August 2000 / Accepted: 14 November 2000 / Published online: 17 February 2001

Abstract This research investigated the effects of an orientation illusion on action, as well as the ability of the motor system to adapt to the illusion. Subjects reached out and picked up a small bar placed at various orientations. A background grating was used to induce an orientation illusion. When the direction of the illusion was reversed, the following seven trials revealed a large illusion effect in the early portion of the reach. In the subsequent seven trials, no effect of the illusion was present. This pattern of adaptation was similar to the pattern often obtained with displacing prisms, suggesting that the two types of visual distortions present the motor system with similar challenges that it meets in similar ways. These findings are consistent with a planning/control model that argues for separate visual representations underlying the planning and on-line control of reaching.

Keywords Optical illusions · Adaptation · Reaching · Planning · Control

Introduction

The question of how the brain converts sensory input into motor output has long been a key issue in motor performance (see, for example, Jeannerod 1988; Soechting and Flanders 1989). In the present study, we examined two aspects of the relationship between vision and action. One aspect concerned the effect of an orientation illusion on the trajectory of a reaching movement, and was studied in order to elucidate how and when in a reach optical illusions might have their effects. Another aspect concerned the ability of the motor system to adapt to an optical illusion over a series of trials.

Motor adaptation to the distorting effects of prisms is a common finding (see, for example, Redding and Wallace 1994, 1997). When prism goggles are first put on, subjects typically misreach in the direction opposite to the visual displacement (exposure effects). Over a number of trials, performance gradually improves until baseline accuracy is regained. When the prisms are removed, subjects initially misreach in the direction opposite to that of their original errors (exposure aftereffects).

Although both optical illusions and prisms can be thought of as visual distortions, they clearly have different origins and effects. Prisms cause a refraction of the light entering the retina, and thus can be considered an “external” distortion. Optical illusions more likely owe their effects to “internal” influences of the context on the perception of the target. Further, whereas prisms displace the entire visual field, an optical illusion is normally focused on a single feature of the target, for example its size, its extent, or its orientation.

Despite the differences between prisms and optical illusions, we hypothesized that the two types of visual distortions might present the motor system with similar problems that are met with in similar ways. In both cases, the brain is confronted with a discrepancy between what is perceived and the required action. If our reasoning is correct, the pattern of adaptation in reaching to a target distorted by an optical illusion ought to be similar to that observed in studies of prism adaptation.

Another issue of interest is the more general effects of illusions on action. Many (though not all) indices of motor performance have been shown to be relatively immune to the perceptual effects of optical illusions [for example, maximum grip aperture (Aglioti et al. 1995) and endpoint accuracy (Bridgeman et al. 1997)]. This has often been held as evidence for separate visual systems underlying perception and action (Aglioti et al. 1995; Bridgeman et al. 1997; Milner and Goodale 1995). However, many indices of action are affected by optical illusions [for example, lifting force (Brenner and Smeets 1996), grasping force (Jackson and Shaw 2000), reaction times (Smeets and Brenner 1995), and movement times (van Donkelaar 1999; Gentilucci et al. 1996; Smeets and

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Brenner 1995)], suggesting that another analysis may be more appropriate.

As an alternative to a perception/action distinction, we suggest that the effects (and non-effects) of optical illusions on action can be understood by distinguishing between action planning and action control (cf. Meyer et al. 1988; Woodworth 1899). In particular, we posit that planning and on-line control use separate visual representations [the “planning/control” model (Glover submitted for publication; Glover and Dixon 2000)]. Planning relies on comparisons of present visual information with past experience in selecting a motor program and is heavily influenced by the context surrounding the target. Control, on the other hand, is specifically concerned with guiding the hand accurately to the target and is largely independent of the context. In support of the planning/control model, we have observed that early portions of a trajectory are more affected by illusions than are later portions [the “dynamic illusion effect” (Glover and Dixon 2000; Glover and Dixon submitted for publication]. The present study was also aimed partly at replicating this effect.

Materials and methods

Subjects

Sixteen University of Alberta undergraduates served as subjects in the experiment. All subjects reported being right-handed and having normal or corrected-to-normal vision. All subjects were naive as to the purpose of the experiment. All gave their informed consent prior to testing.

Apparatus

Subjects sat on an adjustable chair at a 100×60 cm table and viewed the table through a 4×7 cm rectangular area in the center of a two-way mirror. The experimenter manipulated the ability of subjects to see through the mirror by switching on or off the table lighting. When the table was illuminated, subjects were able to see the stimulus through the rectangular viewing area. A high frequency background grating was centered within the subject’s field of view (Fig. 1). On top of the grating was a transparent plastic circle, cut to the same size as the grating, but with a handle attached. On top of the plastic circle was set the target, a 8×2 cm (7° 1′ long by 1° 45′ wide visual angle) black wooden cylinder. A 2×8 cm starting bar was taped to the table, directly in front of the subject. The starting bar was placed with the long axis in line with the sagittal plane of the subjects. The distance between the center of the starting and target bars was 23 cm, and the distance between the center of the starting bar and the subjects’ midsection was roughly 20 cm.

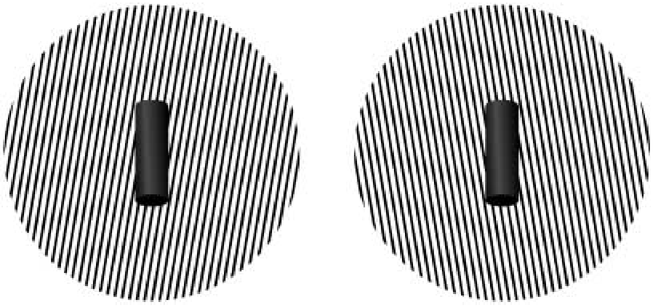

Fig. 1 The orientation illusion used in the present study. On the *left*, the background grating is oriented at –10° from vertical; on the *right*, the background grating is oriented at +10° from vertical. Both bars are drawn vertical, but each appears to be rotated slightly in the opposite direction of the background grating

The table top was monitored with an overhead infrared video camera which fed information into an Iscan tracking system. The tracking system was calibrated using a method adapted from Haggard and Wing (1990). This involved fixing two ireds to a bar at a distance of 12 cm from one another and moving the bar forward and sideways across the workspace from various starting positions while recording the reported distance between the two ireds. The standard deviation of these measurements was less than 1.2 mm in both the forward and horizontal planes.

Experimental procedure

The experimental procedure used in this experiment was approved by the University of Alberta Ethics Review Committee in accordance with the University Standards for the Protection of Human Research Participants and the Canadian Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans.

Perception task

A trial began when the experimenter switched on the lights, making the two-way mirror transparent. The subject had to align the bar with their sagittal plane using the handle attached to the plastic overlay.

In half the trials, the grating was oriented 10° clockwise from the subject’s sagittal plane (“grating +10” condition), and in the other half, it was oriented 10° counterclockwise (“grating –10” condition). Figure 1 shows the two versions of the orientation illusion used. For each grating orientation, the bar was set up in one of ten possible orientations, ranging from +25° to –25° clockwise from sagittal, excluding 0°. In the perception task, subjects received one repetition of each bar and grating orientation combination (presented randomly), for a total of 20 trials. Half of the subjects performed the perception task prior to the reaching task, and the other half performed the perception task after the reaching task.

Reaching task

During the reaching task, subjects wore two ireds attached to their right hand. The ireds were taped to the hand near the large knuckles of the first and fourth fingers, roughly one-third of the distance from the knuckles to the wrist. The ireds were alternately illuminated at 60 Hz, and the position of the lit ired was detected electronically every video frame and recorded by computer for analysis off-line.

Subjects were required to begin each trial by pinching the starting bar between their thumb and fingers. When the table lighting was switched on and the target display was visible through the mirror, subjects were to reach out and pick up the bar near its center using their thumb and finger. They were instructed to place the thumb on the right side of the bar from their perspective. The instructions to the subjects did not emphasize speed. Subjects in the reaching task were given seven practice trials prior to the test trials; the background orientation in the practice trials was opposite to that used during the initial block of test trials. At the start of each trial, the subject’s vision of the reaching hand was limited roughly to the half of the hand near the wrist. Once the reach had been initiated, the subject’s vision of the hand was occluded by the apparatus for roughly the first two-thirds of the movement after it left the starting bar.

The reaching task was divided into eight blocks. The background grating was shifted every block, back and forth between +10° and –10°. Each block was subdivided into two epochs (early and late). Each epoch consisted of a random ordering of seven bar orientations, ranging from +5° to +35° clockwise from sagittal in 5° steps. Half the subjects began with the +10° background and half began with the –10° background.

Post-test questionnaire

After finishing the reaching and perception tasks, subjects completed the Edinburgh handedness inventory (Oldfield 1971). This was done after the testing so as not to arbitrarily exclude subjects from gaining course credit. One subject was excluded because he did not qualify as being strongly right-handed (i.e., laterality quotient >0.67); the remaining 15 were included in the data analysis.

Data analysis

For the perception task, the final orientation to which the subject rotated the bar was scored for each trial. For the reaching task, the dependent variable was the orientation of the hand throughout the course of the reach. Data were analyzed by first passing the position recordings through a custom filter that excluded artifacts. For each video frame, the position of the ired that was not illuminated during that frame was interpolated between the measurements for the succeeding and following frames. The angle between the two ireds was then computed for each sampled position. The criterion velocity for the onset and offset of the movement was set at 0.10 m/s. Trials were excluded if either the reaction time or movement time was less than 250 ms or greater than 1500 ms. Over 90% of trials were included from each subject.

For each movement, the orientation of the hand was computed at 11 equally spaced points from onset to offset, inclusive. These time-normalized data were averaged for each subject, grating and bar orientation, and epoch. The raw illusion effect (the difference in hand orientation between the two grating conditions) was scaled by the corresponding effect of bar orientation at each point in time. The scaled effects were analyzed only for those times for which the slope of the bar orientation effect was greater than 5%.

The results of both tasks were assessed by comparing the fit of nested linear models. The relative quality of two fits was evaluated by computing the maximum likelihood ratio, that is, the likelihood of the data based on one model divided by the likelihood of the data based on the other. This statistic provides a succinct, readily interpretable measure of the quality of the fits without the logical and interpretational difficulties inherent in hypothesis testing (see, for example, Cohen 1994; Loftus 1993). However, likelihood ratios of this sort are closely related to the statistics used in null hypothesis significance testing, and the null hypothesis would generally be rejected when the likelihood ratio is 10 or greater (Dixon 1998; Dixon and O’Reilly 1999). A likelihood ratio of 10 would be classified as “moderate” evidence using the criteria of Goodman and Royall (1988).

Results

Data from the perception task revealed a clear effect of the illusion (2.13°) on performance. A linear model incorporating the effect of background was compared to a null model in which there was no effect of background; this comparison yielded a likelihood ratio of $\lambda>1000$, indicating strong evidence for an effect of background on perceptual judgments. This effect was independent of whether subjects performed the perception task before or after the reaching task; when the effect of order and its interaction with background were incorporated in the model, the fit improved only marginally, yielding a likelihood ratio of $\lambda=7.84$. Because this is less than the criterion of 10 suggested by Dixon and O’Reilly (1999), our interpretation is that there was no clear evidence for an effect of task order on the perception judgments.

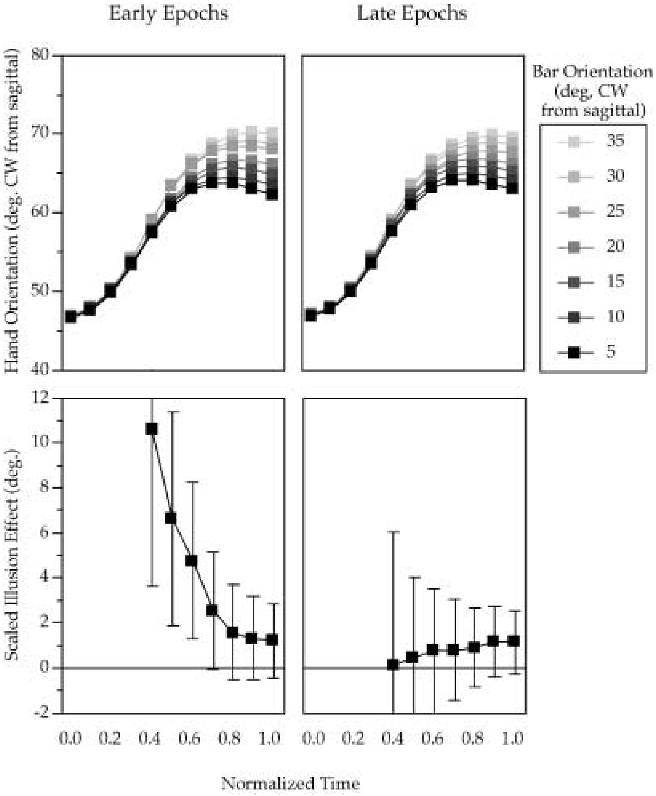

Fig. 2 Orientation of the hand as a function of bar orientation and time (*top*) and illusion effects on hand orientation (*bottom*). Data are shown for the early (*left*) and late (*right*) epochs. Bar effects are shown for each point in normalized time. Illusion effects are shown for each point in normalized time in which the slope of the bar effect is >0.05. *Error bars* represent standard errors of the mean

Figure 2 (*top*) shows the effect of the orientation of the bar on the orientation of the hand in the early (*left*) and late (*right*) epochs. It can be seen that in both epochs, the orientation of the hand became increasingly dependent on the orientation of the bar as the reaches progressed. Figure 2 (*bottom*) shows the scaled effect of the illusion on the orientation of the hand over time in the early (*left*) and late (*right*) epochs. In the early epochs, the illusion had a relatively large initial effect, but this effect decreased to near zero by the time the reach was completed. In the late epochs, there appeared to be no effect of the illusion on hand orientation at any time during the reach. In the best fitting linear model, it was assumed that the illusion effect was different in early and late epochs and that this difference varied over time. Likelihood ratios indicated that this model fit the data more accurately than several simpler alternatives. The likelihood ratio comparing this model with a null model that did not include effects of time and epoch was λ>1000. When compared to a model that included only an effect of time, the likelihood ratio was λ=471.0. When compared to a model that included only additive effects of time and epoch, the likelihood ratio was λ=33.7. Thus, the results provide strong support for an effect of epoch that varies over time.

Discussion

Two results of the present study are of importance. First, the presence of an illusion effect that decreases over time in the early epochs of the reaching task supports the planning/control model. In this model, it is assumed that planning an action is affected by the context surrounding the target, whereas on-line control is not. We have observed this pattern of effects previously using a design in which the sign of the orientation illusion varied randomly from trial to trial (Glover and Dixon 2000; Glover and Dixon submitted for publication), although the effects in the early epochs of the present study were approximately twice as large. Further, we have also observed the dynamic illusion effect when vision of the hand and target was removed during reaching (Glover and Dixon submitted for publication), showing that the on-line correction of the illusion effect does not depend on visual feedback. The present study does not support the view that perception and action rely on separate visual representations and that perceptions are more affected by illusions than actions (Milner and Goodale 1995).

The planning/control model provides a useful framework for interpreting the pattern of illusion effects on action found in this study as well as in the literature as a whole; however, there appear to be many factors involved. For example, illusions clearly have greater effects when movements are initiated after a delay of 2 s or more from the offset of the visual stimulus (Gentilucci et al. 1996; Westwood et al. 2000; Wong and Mack 1981). Further, illusions may have greater effects under monocular viewing conditions (Marotta et al. 1998; but see Otto-de Haart et al. 1999). Illusions may also have greater effects on grasping than on reaching (Aglioti et al. 1995; Bridgeman et al. 1997; Haffenden and Goodale 1998; Vishton et al. 1999), and their effects on action can be larger when visual feedback is unavailable (Gentilucci et al. 1996; Westwood et al. 2000). Although these results can be accommodated within the planning/control model (Glover submitted for publication; Glover and Dixon 2000), they also point to the complexity of the interplay among factors.

The results of the present study could also be incorporated within the perception/action model if one assumes that the two visual systems interact during some actions. For example, the ventral stream, normally involved in perception, might contribute to the planning of actions in situations such as when the target's function or weight must be considered. On this analysis, the large effect of the orientation illusion in the early portion of the reaches in the present study might be assumed to reflect the use of the ventral (perception) stream in the planning stage. The decline in the effect of the illusion as the hand approaches the target might reflect the dorsal (action) stream's control of the movement on-line. Although an interaction of this sort can be used to accommodate the results of the present study, our view is that a distinction between planning and control seems to explain the results somewhat more parsimoniously.

The second important result of the present study is the lack of an illusion effect in the late epochs of the reaching task. This supports the hypothesis that the motor system can adapt to an illusion over a series of trials when the direction of the illusion is consistent. This pattern of results is comparable to the adaptation effects observed when subjects wear prism goggles. These similarities suggest that the motor system may adapt to these two types of visual distortions in a comparable way, despite their distinct origins and effects.

Several possible interpretations concerning the nature of this adaptation process have been suggested. One is that, during adaptation, one or more proprioceptive maps are "re-aligned" to the visual map (see, for example, Redding and Wallace 1994, 1997). In the present case, this would mean that the "felt" orientation of the hand is being adapted to the visually perceived orientation of the target over a series of trials. A second possibility is that the motor output is changed to achieve the desired result but without any change in the proprioceptive or visual maps (efference theories; see, for example, Taub 1968). A third possibility is that the visual perceptions change (von Helmholtz 1962). In the present case, visual effects would presumably be restricted to the perception of the bar's orientation and would exclude changes in the perception of any of its other features. Finally, it may be that some combination of these changes goes on simultaneously.

The present study does not allow us to make claims as to the nature of the adaptation. Nor would we assume that the source of the adaptation demonstrated here is necessarily identical to that when subjects wear prism goggles. Yet the present study does clearly demonstrate that the motor system can adapt to an optical illusion, and that the pattern of effects is similar to the pattern observed when subjects adapt to prism goggles. This result is broadly consistent with the view that planning an action is based on memories of past experience, and that such experience allows the planning system to adapt to a visual distortion regardless of its origins

Acknowledgements This research was supported by the Natural Science and Engineering Research Council of Canada, through a scholarship to the first author, and a grant to the second author. Parts of this research were previously reported at the Annual Meeting of the Psychonomic Society, Los Angeles, 1999

References

Aglioti S, De Souza J, Goodale M (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Brenner E, Smeets J (1996) Size illusion influences how we lift but not how we grasp an object. Exp Brain Res 111:473–476

Bridgeman B, Perry S, Anand S (1997) Interaction of cognitive and sensorimotor maps of space. Percept Psychophys 55:456–469

Cohen J (1994) The Earth is round ($P<0.05$). Am Psychol 49:997–1003

Dixon P (1998) Why scientists value *P* values. Psychonom Bull Rev 5:390–396

Dixon P, O'Reilly T (1999) Scientific versus statistical inference. Can J Exp Psychol 53:133–149

Donkelaar P van (1999) Pointing movements are affected by size-contrast illusions. Exp Brain Res 125:517–520

Gentilucci M, Chieffi S, Daprati E, Saetti M, Toni I (1996) Visual illusion and action. Neuropsychologia 34:369–376

Glover SR, Dixon P (2000) Dynamic illusion effects in a reaching task: evidence for separate visual systems in the planning and control of reaching. J Exp Psychol Hum Percept Perform (in press)

Goodman SN, Royall R (1988) Evidence and scientific research. Am J Public Health 78:1568–1574

Haffenden AM, Goodale M (1998) The effect of pictorial illusion on prehension and perception. J Cogn Neurosci 10:122–136

Haggard P, Wing A (1990) Assessing and reporting the accuracy of position measurements made with optical tracking systems. J Motor Behav 22:315–321

Helmholtz H von (1962) Helmholtz's treatise on physiological optics. Dover Press, New York

Jackson SR, Shaw A (2000) The Ponzo illusion affects grip force but not grip aperture scaling during prehension movements. J Exp Psychol Hum Percept Perform 26:418–423

Jeannerod M (1988) The neural and behavioral organization of goal-directed movements. Oxford University Press, Oxford, UK

Loftus GR (1993) A picture is worth a thousand *P* values: on the irrelevance of hypothesis testing in the microcomputer age. Behav Res Methods Instrum Comp 25:250–256

Marotta JJ, DeSouza J, Haffenden A, Goodale M (1998) Does a monocularly presented size-contrast illusion influence grip aperture? Neuropsychologia 36:491–497

Meyer DE, Abrams R, Kornblum S, Wright C, Smith K (1988) Optimality in human motor performance: ideal control of rapid aimed movements. Psychol Rev 95:340–370

Milner AD, Goodale M (1995) The visual brain in action. Oxford University Press, Oxford, UK

Oldfield R C (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Otto-de Haart EG, Carey D, Milne A (1999) More thoughts on perceiving and grasping the Muller-Lyer illusion. Neuropsychologia 37:1437–1444

Redding GM, Wallace B (1994) Effects of movement duration and visual feedback on visual and proprioceptive components of prism adaptation. J Motor Behav 26:257–266

Redding GM, Wallace B (1997) Prism adaptation during target pointing from visible and nonvisible starting locations. J Motor Behav 29:119–130

Smeets JB, Brenner E (1995) Perception and action are based on the same visual information: distinction between position and velocity. J Exp Psychol Hum Percept Perform 21:19–31

Soechting JF, Flanders M (1989) Sensorimotor representations for pointing to targets in three-dimensional space. J Neurophysiol 62:582–594

Taub E (1968) Prism compensation as a learning phenomenon: a phylogenetic perspective. In: Freedman S (ed) The neuropsychology of spatially oriented behavior. Dorsey, Homewood, IL

Vishton PM, Rea J, Cutting J (1999) Comparing effects of the horizontal-vertical illusion on grip scaling and judgment: relative versus absolute, not perception versus action. J Exp Psychol Hum Percept Perform 25:1659–1672

Westwood DA, Heath M, Roy E (2000) The effect of a pictorial illusion on closed-loop and open-loop prehension. Exp Brain Res 134:456–463

Wong E, Mack A (1981) Saccadic programming and perceived location. Acta Psychol 48:123–131

Woodworth RS (1899) The accuracy of voluntary movements. Psychol Rev Mono Suppl 3