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RESEARCH ARTICLE

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Effects of an orientation illusion on motor performance and motor imagery

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Abstract Although the effect of visual illusions on overt actions has been an area of keen interest in motor performance, no study has yet examined whether illusions have similar or different effects on overt and imagined movements. Two experiments were conducted that compared the effects of an orientation illusion on an overt posture selection task and an imagined posture selection task. In Experiment 1 subjects were given a choice of grasping a bar with the thumb on the left side or right side of the bar. In Experiment 2 subjects were instructed to only imagine grasping the bar while remaining motionless. Subjects then reported which side of the bar their thumb had been placed in imagined grasping. Both the overt selection and imagined selection tasks were found to be sensitive to the orientation illusion, suggesting that similar visual information is used for overt and imagined movements, with both being sensitive to an orientation illusion. The results are discussed in terms of the visual processing and representation of real and imagined actions.

Introduction

Recent studies have catalogued a range of circumstances in which visual illusions may or may not affect actions. Specifically, illusions have been shown to affect characteristics of movement that depend on target weight (Brenner and Smeets 1996), movements made after a delay (Bridgeman et al. 1997; Gentilucci et al. 1996), and the early portions of movements made under either closed-loop or open-loop (no delay) conditions (Brouwer et al. 2003; Glover and Dixon 2001a, b; Heath et al. 2004). In contrast, illusions seem to have much smaller or no effects on characteristics of movement that arise late in a movement, for example maximum grip aperture (Aglioti et al. 1995; Haffenden et al. 2001) and the accuracy of pointing or hitting movements (Bridgeman et al. 1997; Brouwer et al. 2003; Gentilucci et al. 1996).

One of the problems with comparing the effects of a visual illusion on perceptions and actions relates to the fact that the latter invariably allows performance feedback whereas the former typically does not. That is, when participants act on objects subject to a visual illusion, any error in performance can be detected by either:

– visual comparison of the hand and target; or
– use of haptic feedback from the hand.

Although some studies have avoided the problem of a direct visual comparison between hand and target by conducting movements in a visual open loop, the problem of haptic feedback remains largely unresolved.

However, unlike tasks such as reaching and grasping, motor imagery does not allow for haptic feedback on performance. In a reaching and grasping task, when the hand contacts a target subject to a visual illusion, any illusion-induced error that exists at that point can potentially inform the motor system through feedback from receptors in the hand and fingers. Haptic feedback has been shown to play a critical role in motor learning (Gentilucci et al. 1995), and could potentially reduce or eliminate effects of illusions on motor planning. This type of motor learning was evident in a study that showed that reaching movements could adapt to an orientation illusion over a number of trials (Glover and Dixon 2001a). Thus, examination of the effects of a visual illusion on motor imagery provides a potentially valuable area of

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study, because motor imagery provides a relatively pure, execution-free index of motor planning.

In this study we explored the effects of a visual illusion on motor imagery. We ran two experiments involving a bar placed at different orientations. We previously demonstrated that an orientation illusion affects the choice of grasping posture under comparable circumstances (Glover and Dixon 2001b), and Experiment 1 was designed both to test the reliability of this finding and to provide a baseline with which to compare performance in Experiment 2. In Experiment 2 subjects were required to imagine grasping the bar while remaining motionless and then to subsequently report the posture they had used in the imagined grasp. This enabled measurement of the effects of the illusion on motor imagery.

In both tasks the perceived orientation of the bar was manipulated via a background grating. When the grating was oriented 10° clockwise from the sagittal plane, it led to a corresponding misestimate of the bar's orientation in the counter clockwise direction, and vice-versa (Fig. 1). A range of bar orientations was employed that encouraged the participants to adopt a "thumb-left" posture (for grasping the bar in extreme counter-clockwise orientations) or a "thumb-right" posture (for extreme clockwise orientations) (Fig. 2). Under such conditions subjects will tend to switch from one posture to another at an intermediate orientation (Glover and Dixon 2001b; Johnson 2000; Rosenbaum et al. 1992). Further, because it is awkward and costly to change one's choice of postures in mid-flight (Stelmach et al. 1994), posture choice most probably reflects the output of pre-movement planning processes alone. Because performance in motor imagery tasks has been shown to closely resemble performance in real grasping tasks under similar conditions, we used the same apparatus and stimuli for both tasks.

Experiment 1

Method

Subjects

Ten volunteers participated in the study in return for redeemable vouchers. Subjects all had normal or corrected-to-normal vision and were right-handed by self-report. All subjects gave their informed consent, and all were naïve about the exact purpose of the experiment. The procedures were approved by the Oxfordshire Regional Ethics Committee (OxREC No. C02.092).

Apparatus

Subjects were seated comfortably at a large wooden table, 75 cm high, 120 cm wide, and 82 cm in the depth plane. They sat facing an 8 cm×2 cm×2 cm wooden bar, painted white. The target bar was placed 41 cm from the edge of the table nearest the subject. The target bar had two small holes drilled in the bottom (invisible to the subject) that enabled it to be situated snugly on two small cylinders that protruded from a hole cut through the table. The cylinders themselves were attached to a motor that was screwed to the underside of the table. The motor was controlled via computer and could be used to rotate the bar, in steps of 5°, between 5 and 35° clockwise from the subjects' sagittal plane. The target bar sat on top of a square (17 cm×17 cm) grating. The grating consisted of equally sized alternating black and white lines, with a frequency of 1.76 lines cm^{-1}. The grating was fit loosely over the cylinders, enabling it to be rotated by the experimenter.

An 18 cm×9 cm×2 cm (in height) box containing a start key was fastened to the table using Velcro fasteners directly in front of the subjects' midsection, such that the centre of the start key was 8 cm from the edge of the table closest to the subject. The start key was 8 cm wide in the horizontal plane of the subject and 2 cm wide in the frontal plane, and protruded approximately 2 cm above the top of the box. Attached to the top of the start key, and centred on it, was a 6 cm×2 cm×2 cm wooden bar, painted white. This starting bar was positioned parallel with the subjects' sagittal plane.

Procedure

Subjects began each trial with their eyes closed, grasping the starting bar by the ends, and pressing down on the start key. Pressing the start key signalled the computer to begin the next trial. One second after the key was

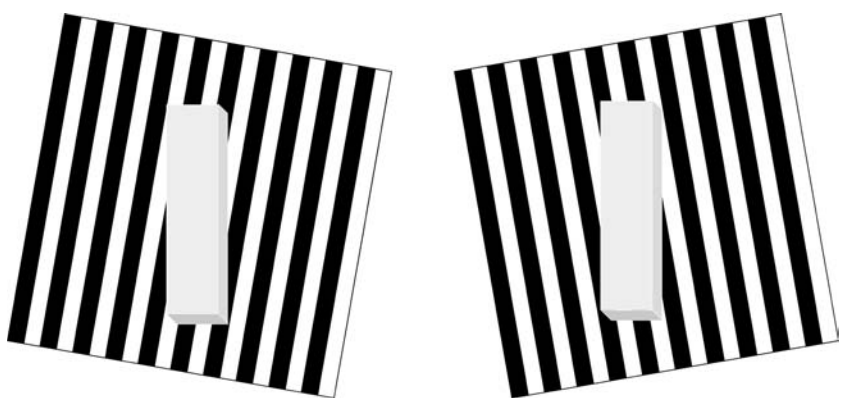

Fig. 1 The orientation illusion used in this study. On the *left*, the background grating is oriented at +10° clockwise from sagittal, on the *right* the grating is oriented at −10°. Both *bars* are drawn at +20°, but each appears to be tilted slightly in the direction opposite the grating

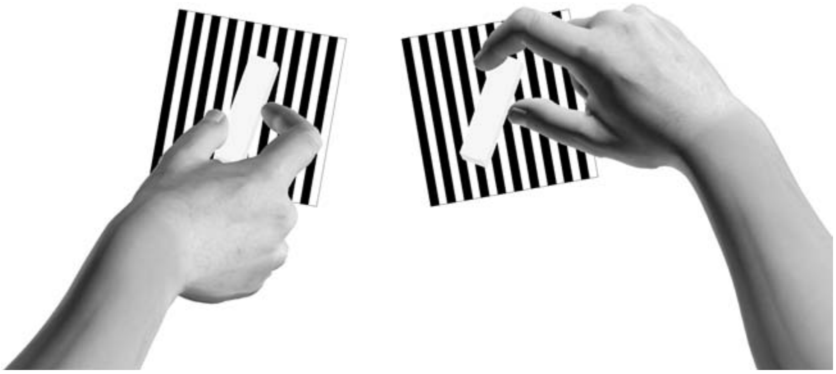

Fig. 2 The 'thumb-left' and 'thumb-right' postures allowed in this task. The thumb-left posture (*left panel*) is most comfortable when the *bar* is oriented far from the sagittal plane, the thumb-right posture (*right panel*) is most comfortable when the *bar* is oriented near to the sagittal plane

pressed the computer-controlled motor rotated the bar to its orientation for the next trial. Also during this period, the experimenter rotated the background, so that it was oriented at either ±10° clockwise from sagittal. One second after the bar had been rotated the computer sounded a tone signalling subjects to open their eyes. A second tone was sounded two seconds later, signalling subjects to reach out and grasp hold of the target bar using their thumb and index fingers only. Subjects were required to grasp the bar roughly halfway along its length with the thumb and finger on opposite sides of the bar. They were instructed not to lift the bar, but only to grasp it. Before the start of the experimental trials, subjects were shown the two possible ways of grasping the bar (thumb-left or thumb-right) and were allowed six practice trials with each type of grasp. The background was set at 0° for these practice trials and the orientation of the bar was determined randomly. When they had completed the grasp, they were required to return to the start position, close their eyes, and press down again on the start key.

Each subject completed 140 trials. For each combination of bar orientation (5, 10, 15, 20, 25 30, and 35°) and background orientation (±10°), there were 10 repetitions, pseudo-randomly determined.

Data analysis

Data were analysed using log linear models that predicted the log odds of posture choice as a linear function of bar orientation, background grating orientation, and subject. Log linear modelling uses an iterative procedure to maximize the likelihood of the data given the parameter estimates. To approximate the treatment of subjects as a random effect, the log odds were first normalized for overall differences across subjects in the use of the postures by entering subjects as a factor first and then adjusting the likelihood for the loss of those degrees of freedom. (This procedure is analogous to the treatment of random effects in linear modelling.) The crucial comparison was then between a model that included an effect of bar orientation and one that included background grating and bar orientation. The relative fit of the models was assessed by calculating the ratio of the likelihoods for the two models, λ. To compensate for the additional degree of freedom for background grating in the second model, the likelihood ratio was adjusted in a manner equivalent to the treatment of degrees of freedom in the Bayesian Information Criterion (Glover and Dixon 2004). Comparing models using likelihood ratios in this way provides a convenient, intuitive means of data analysis and presentation that avoids the pitfalls commonly associated with null hypothesis significance testing (Dixon 1998, 2003; Glover and Dixon 2004;). By way of comparison, an adjusted likelihood ratio of three would be sufficient to reject the null hypothesis with $\alpha = 0.05$ in some prototypical hypothesis testing situations and would be regarded as "moderate to strong" evidence in favour of one model over another by Goodman and Royall (1988).

Results and discussion

Figure 3 shows the probability of grasping the bar with the thumb on the right as a function of bar and grating orientation. It is clear from the figure that, as the bar was rotated further from the subjects' sagittal plane, the participants were more likely to grasp the bar with the thumb on the left. Further, the analysis showed that this effect also depended on the orientation of the grating. When the grating was oriented at −10° clockwise from sagittal (making the bar appear oriented further clockwise from sagittal), participants were also more likely to grasp the bar with their thumb on the left than when the grating was oriented at +10° from sagittal (making the bar appear oriented nearer to sagittal). The likelihood ratio comparing a model that included an effect of both bar and grating orientations (after normalizing for the random effect of subjects) to a model including only an effect of bar orientation was $\lambda = 12.0$, even after adjusting for the additional degree of freedom. In other words, the data were 12 times as likely on the assumption that both the bar and grating affected participants' choices of postures than on the assumption that only the bar affected posture.

The log linear modelling procedure estimated the log odds of response choice as a linear function of bar angle and background. The parameter estimate for the effect of bar angle was 0.24 per degree of orientation. On the

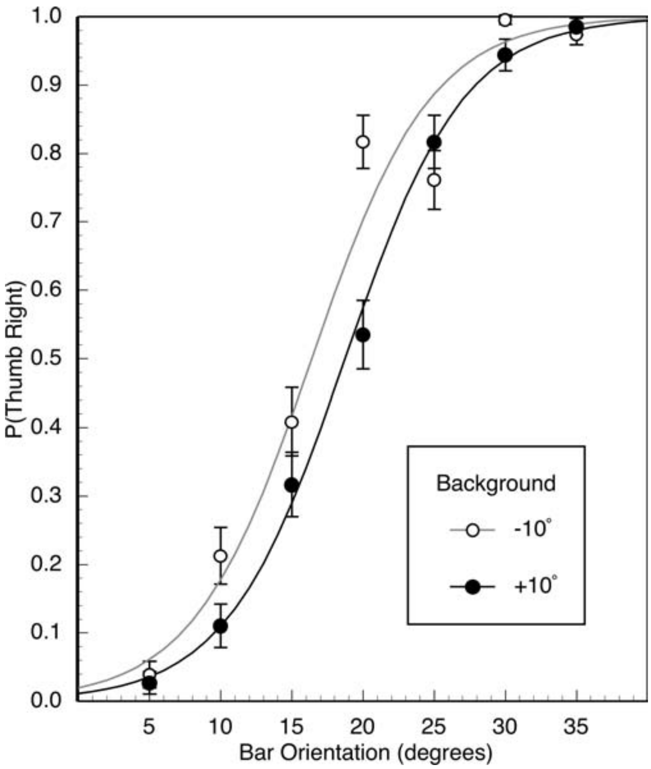

Fig. 3 Experiment 1: Percentage of trials in which the "thumb-left" posture was selected as a function of bar orientation and background grating orientation. The bar orientation is presented in five-degree steps along the *x*-axis. The background grating orientation was either −10° (*black circles*) or +10° (*white circles*)

other hand, the parameter estimate for the effect of background was 0.28 for a 10° shift in the background, or 0.028 per degree. Thus, shifting the background had an effect on response choice that was approximately 12% as large as that of physically shifting the bar the same amount.

The results of this experiment replicated those found by Glover and Dixon (2001b), in which an orientation illusion was shown to affect posture selection. These results support the notion that motor planning is affected by the visual illusion because posture selection represents a movement parameter that is largely preplanned and difficult to adjust in flight. The results of Experiment 1 also provided a baseline with which we could compare performance in motor imagery task of Experiment 2.

Experiment 2

Methods

Subjects

Ten volunteers participated in the study in return for redeemable vouchers. None of these subjects had participated in Experiment 1. Subjects all had normal or corrected-to-normal vision and were right-handed by self-report. All subjects gave their informed consent, and all were naïve about the exact purpose of the experiment. The procedures were approved by the Oxfordshire Regional Ethics Committee (OxREC No. C02.092).

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

The procedure was identical to that used in Experiment 1 except that in each trial subjects were instructed to imagine grasping the target bar with their right hand while remaining motionless. After each trial subjects had to report which side of the target bar their thumb had been placed on (left or right) during imagined grasping.

Data analysis

Data analysis was identical with Experiment 1, except that the dependent variable was now the reported posture used in imagined grasping. A second analysis was conducted that combined the data from the two experiments to assess the difference between real and imagined grasping.

Results and discussion

Figure 4 shows the data from Experiment 2. Analogous to the real grasping task of Experiment 1, the further the bar was rotated from the participants' sagittal plane, the more likely they were to report having imagined grasping it with their thumb on the right. This resemblance across experiments is consistent with the view that motor imagery of posture choice operates analogously to actual motor planning, as suggested by previous studies (Frak et al. 2001; Johnson 2000).

The first analysis concerned the effect of the background grating on motor imagery. Here, a model incorporating an effect of both bar and grating orientation with a random effect of participants fit the data much better than a model incorporating only the effects of bar and participants, $\lambda > 1000$. That is, the data were more than 1000 times more likely on the assumption that both the bar and grating affected the posture selected than on the assumption that only the bar affected the posture selected. The results of Experiment 2 are thus strong evidence that motor imagery is susceptible to an orientation illusion.

As in Experiment 1, the magnitude of the effect of the illusion can be compared with the effect of physical bar orientation. The parameter estimate for the effect of bar angle in the log linear model was 0.26 per degree of orientation. On the other hand, the parameter estimate for the effect of background was 0.42 for a 10° shift in

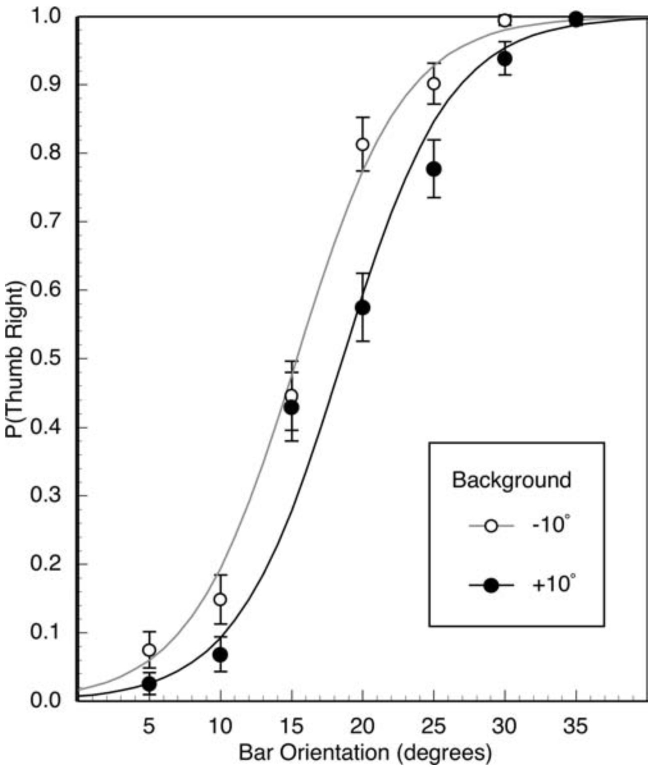

Fig. 4 Experiment 2: Percentage of trials in which subjects reported using a ''thumb-left'' posture in imagined grasping. Conventions as for Fig. 3

the background, or 0.042 per degree. Thus, shifting the background had an effect on response choice that was about 16% as large as that of physically shifting the bar the same amount. This estimate is slightly larger than the 12% estimate found in Experiment 1.

In the second analysis, the results from both experiments were pooled. In this case, the adjusted likelihood ratio indicated strong evidence for an overall effect of background, $\lambda > 1000$. This was expected, given that each experiment provided clear evidence for an effect independently. More critically, there was no evidence that the effect of background differed in the two procedures. In fact, when adjusted for the additional degree of freedom as before, the likelihood ratio was $\lambda = 38.1$ in favour of the simpler model in which the orientation of the background grating had the same effect on imagined and real grasping posture.

General discussion

We here examined the effects of an orientation illusion on both motor planning and motor imagery. In Experiment 1, the illusion affected the way in which participants reached out to grasp the bar. Specifically, when the background grating was positioned so as to make the bar appear to be oriented further from the sagittal plane than its true orientation, participants were more likely to grasp the bar with the thumb on the right, just as if it actually had been oriented further from their sagittal planes. The reverse was also true: when the orientation of the bar was made to appear closer to the sagittal plane, participants were more likely to grasp it with their thumb on the left.

A similar result was obtained for the motor imagery task of Experiment 2 in which participants were instructed to only imagine they were grasping the bar and remained motionless throughout the course of each trial. Indeed, the results from the combined analysis indicated that the background had an equivalent effect in the two procedures.

These results are consistent with at least three models of illusions and action. First, the planning-control model holds that illusions should affect planning but not on-line control (Glover and Dixon 2001a). Within this framework, motor imagery is posited to rely on similar representations as are involved in motor planning (Glover 2004). It is argued that motor imagery involves a planning phase utilising available visual information, but not an execution phase, because on-line visual and proprioceptive feedback are never obtained. Similarly, as posture choice represents a movement parameter that is costly and awkward to adjust in flight (Stelmach et al. 1994), it probably reflects the outcome of pre-movement planning processes alone, independent of on-line control. The equivalent effects of the orientation illusion in the motor imagery task are consistent with the notion that motor planning and motor imagery utilise similar processes involving similar visual information.

Second, the effect of the illusion on posture choice may also be consistent with a model that suggests that the orientation illusion used here originates early in the visual system and thus affects perceptions and actions equally (Milner and Goodale 1995). Assuming this model also holds that motor imagery can be included as a form of ''action'', then the results of the present study are understandable. Finally, the effects of the illusion on both posture choice and motor imagery are also consistent with the common-representation model of Franz et al. (2001). In that model, illusions should affect all behaviour, be they perceptual judgments, overt actions, or motor imagery.

Whereas the orientation illusion used here seems to have equal effects on motor performance and motor imagery, it is not yet known whether such results would be obtained for other illusions and other types of task. It is certainly within the realm of possibility that certain illusions may affect motor imagery and perceptions, but not overt actions, given the presence of haptic feedback in the lattermost tasks. It is unknown which illusions and tasks will lead to the greatest effects, though it is interesting that some illusions such as the Muller–Lyer and the orientation illusion used here tend to have larger effects on actions than do others such as the Ebbinghaus illusion. One possible explanation of these differences is that the Muller–Lyer owes at least some of its effects to the blurring of the endpoints at the retinal level.

Similarly, the orientation illusion may tend to have larger effects on action because it originates earlier in the visual system.

The issue of how and when visual illusions affect actions continues to be an area of controversy in the field of motor performance. In this study we have shown for the first time that an illusion can affect not just how one performs an action, but also how one would imagine performing the action. Further, the results indicate that the illusion had a similar effect on both motor imagery and action performance. Whether or not the illusion effects observed here can be generalized to other illusions and other motor imagery tasks is an open question. This issue may have important implications for our understanding of visual processing and motor representation.

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