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Research Report

Dissociation of perception and action unmasked by the hollow-face illusion

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ABSTRACT

It has been suggested that there are two separate visual streams in the human cerebral cortex: a ventral pathway that provides perceptual representations of the world and serves as a platform for cognitive operations, and a dorsal pathway that transforms visual information for the control of motor acts. Evidence for this distinction comes from neuropsychology, neuroimaging, and neurophysiology. There is also evidence from experimental psychology, with normal observers experiencing an illusion—where perception and action can be dissociated, although much of this evidence is controversial. Here, we report an experiment aimed at demonstrating a large dissociation between perception and fast action using the hollow-face illusion, in which a hollow mask looks like a normal convex face. Participants estimated the positions of small targets placed on the actually hollow but apparently normal face and used their fingers to 'flick' the targets off. Despite the presence of a compelling illusion of a normal face, the flicking movements were directed at the real, not the illusory locations of the targets. These results show that the same visual stimulus can have completely opposite effects on conscious perception and visual control of fast action.

1. Introduction

The notion of an ancient visual system for rapid action and a more recent visual system for (conscious) cognitive operations, such as planning, makes evolutionary sense (Goodale and Milner, 1992; Milner and Goodale, 1995). Present evidence for these two streams–believed to be organized into dorsal and ventral cortical pathways respectively–comes from rare patients with selective brain lesions (Goodale et al., 1991; Perenin and Vighetto, 1988), neuroimaging studies (Culham and Kanwisher, 2001; Grill-Spector, 2003), and neurophysiology (Cohen and Andersen, 2002; Tanaka, 2003).

The two-streams hypothesis has also received support from somewhat controversial behavioral studies that have examined the influence of perceptual illusions on the control of object-directed actions such as saccades, reaching movements, and grasping (for reviews, see (Goodale and Milner, 2004; Goodale and Westwood, 2004)). Early experiments showed that saccadic eye movements are insensitive to a dot-in-frame illusion in which the perception of a target's location is shifted opposite to the displacement of a large visual frame (Bridgeman et al., 1981; Wong and Mack, 1981), suggesting that location is processed differently by the visuomotor and perceptual systems. Aglioti et al., (1995) later demonstrated that the maximal opening of a grasping hand is

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insensitive to the robust perceptual illusion that a target disk surrounded by smaller circles is larger than the same disk surrounded by larger circles (Ebbinghaus Illusion)—despite the fact that grip opening is exquisitely sensitive to real changes in the size of the target disk. Peak grasping aperture is refractory to this size contrast illusion even when the hand and target are occluded during the action (Haffenden and Goodale, 1998), indicating that on-line visual feedback during grasping is not required to 'correct' an initial perceptual bias induced by the illusion.

A number of recent findings, however, have challenged the notion that perceptual illusions do not affect the control of object-directed actions. These challenges fall into several categories including: non-replication (Franz et al., 2003), the contention that early studies did not adequately match action and perception tasks for various input, attention, and output demands (Bruno, 2001; Smeets and Brenner, 2001; Vishton, 1999), or the idea that action tasks involve multiple stages of processing from purely perceptual to more 'automatic' visuomotor control (Glover, 2004; Glover and Dixon, 2001). Some of the competing accounts (Glover, 2004; Smeets and Brenner, 2001) are difficult to separate from the original two-streams proposal. In addition, some of the contradictory findings (Glover and Dixon, 2001) can be explained by appealing to the fact that illusions can arise at different stages in visual processing (Dyde and Milner, 2002). According to this argument, illusions that arise in early visual areas, such as primary visual cortex, will have an effect on action, whereas illusions that arise at higher stages of visual processing in the ventral stream will not. Nevertheless, because the illusory distortions that have been used in all the studies to date were no more than a few millimeters, the experiments were technically difficult to carry out and this could explain why the results have sometimes been hard to replicate (Franz et al., 2003). Thus, a large visual illusion (preferably many centimeters) that nevertheless shows a clear dissociation between perceptual report and action would be reassuring.

We looked for a dissociation between conscious perception and rapid action using the large and dramatic depth reversal of the hollow face, in which a realistic hollow mask appears as a convex face (Gregory, 1970). This is evidently a knowledge-based, top–down effect, where extensive and powerful (though implicit) knowledge of convex faces rejects the correct hollow perception in favor of reversed depth (Gregory, 1997). According to the two-streams hypothesis, the cognitive hollow-face illusion arises within the ventral stream and should therefore not affect visuomotor computations in the dorsal stream (Dyde and Milner, 2002). Although the hollow-face illusion is strong, it can be countered by powerful opposed bottom–up information, especially binocular information from close viewing with both eyes (Hill and Bruce, 1993), or less effectively by shape-from-shading, with strong overhead illumination of the hollow mask (Hill and Bruce, 1993; Ramachandran, 1988).

The main question was this: would rapid hand movements be directed to touch the real position of the mask or (wrongly) to the illusorily reversed mask? The two-streams hypothesis would predict that fast (and automatic) movements (mediated by the dorsal system) would be directed to touch the truly concave face, despite the presence of a compelling illusion of a convex face (mediated by the ventral stream). To test this, we asked participants to reach out rapidly and flick off targets that were placed on the mask.

We also asked our participants to make slower and more deliberate pointing movements to these same targets. We did this because an earlier study had reported that pointing movements to a stereoscopic pair of pictures of a 3-D virtual-reality hollow mask were directed at the perceived position of the display, corresponding to the apparent reversed depth (Hartung et al., 2005). There is evidence, however, that pointing movements can often be influenced by cognitive factors and need not engage the 'automatic' mechanisms in the dorsal stream (Bridgeman et al., 1997). In fact, neurological patients with dorsal-stream damage, who cannot reach out accurately to acquire targets using rapid 'automatic' movements, can sometimes improve their performance dramatically if they are encouraged to slow down and move more deliberately, thereby (it has been argued) engaging 'perceptual' mechanisms in the ventral stream (Rossetti et al., 2005). This might explain why the participants in the earlier study Hartung et al., (2005) pointed to the perceived (i.e., the illusory) location of the mask. We expected our participants to behave the same way when making slow and deliberate pointing movements to the targets placed on the mask. In contrast, we expected that participants would direct their rapid flicking movements to the veridical locations of the targets, showing no sensitivity to the concurrent illusion of depth.

2. Materials and methods

2.1. Participants

Eight right-handed participants (mean age 23 years) were tested. All participants reported normal or corrected-to-normal visual acuity and were either compensated financially for their time or given a course credit. They gave their informed consent prior to testing. The experiment was approved by The Review Board for Non-Medical Research Involving Human Subjects (at the University of Western Ontario) and was carried out in accordance with the principles of the Helsinki 1964 Declaration.

2.2. The experimental conditions and responses

There were three experimental conditions: (1) a normal convex face mask seen as a normal face, (2) a hollow mask seen as an illusion—looking convex and not hollow, and (3) a hollow mask seen as a hollow face.

There were three measured responses: (1) fast "flicking" movements with the finger to targets on the face, (2) slow pointing movements with the finger to the perceived locations of targets on the face, and (3) drawing of the target positions on paper (relative to a reference plate). In all three cases, the dependent measure was the horizontal displacement (distance in the Z dimension of depth) with respect to the reference plate.

2.3. The mask displays and their presentation

The stimuli were two female face masks, identical except that one was convex and the other concave (22.8 cm long and 14.8 cm wide). Sheet metal was glued to the backs of the masks, so small target magnets could be placed on their front surfaces. The faces were mounted on a 'reference plate', such that the normal (convex) face protruded in front and the hollow face receded behind it. The displays were mounted firmly on a rotatable turret as shown in Fig. 1. The device allowed us to present one mask at a time by rotating it to either one of two settings.

A sliding mechanism allowed us to move the entire display on each trial to one of 3 randomized distances (19.8, 24.8, and 29.8 cm from the start button) to prevent participants from making stereotyped movements. A single target–a small cylindrical magnet (0.4 cm long and 0.5 cm in diameter) covered with white cloth tape–was presented at two different depth locations on the faces: the side of the cheek (1.1 cm from the reference plate) or the forehead (5.5 cm from the reference plate). The displays were sufficiently large that participants could flick the targets from the hollow face without colliding with the edge of the mask. In other words, the same type of reaching movements could be used to flick targets off either the normal or the hollow face.

2.4. The viewing conditions

The hollow-face illusory depth reversal is robust, except when countered by strong stereo information in near viewing with both eyes. As the mask had to be sufficiently near in this experiment for the participant to reach the targets, this was a problem. Hence, we reduced the countering stereo by filtering out high spatial frequencies, with a de-focusing lens placed over the non-dominant eye, which allowed only low-frequency binocular information. The lens was selected individually to preserve the illusion within reaching distance. The first lens tried was always −3.75 diopters, a value that was found to be optimal in three individuals tested in an earlier pilot study. Subsequently, stronger or weaker lenses were employed until the participant reported a strong and immediate illusion. As it turned out, the mean lens strength used in the experiment was also −3.75 diopters.

Testing took place in a dark room where the only source of illumination was a hidden spotlight. The direction of lighting, and/or its intensity, was different for each experimental condition. The hollow mask, seen illusorily as convex, was illuminated from below by a small spotlight. To keep shadow information similar, the spotlight was placed above the normal mask. In one final condition, the illusion for the hollow mask was abolished by bright overhead lighting and by removing the de-focusing lens.

2.5. Procedure

Each behavioral measure (fast flicking, deliberate pointing, and paper-and-pencil drawing) was tested in separate blocks of trials. In the first part of the experiment, the normal face and hollow face looking illusory were randomly interleaved in a different order for each participant. In the last part of the experiment, the hollow face looking hollow was presented on its own.

The fast flicking and slow pointing were performed in visual open loop (no visual feedback after the finger left the start button). LCD (PLATO) goggles were used to control the viewing time: the face display was revealed and then, after 3 s, a start signal was given to initiate the participant's fast flicking, or slow pointing, movement to the target. The goggles became opaque as soon as the moving finger left the start button.

Fast flicking: Participants were asked to flick the small magnet off the face as quickly and accurately as they could, using their index finger. These flicking movements were measured with an optoelectronic system (OPTOTRAK 3020: Northern Digital), which recorded (at 200 Hz) the position of an infrared emitting diode located at the base of the index finger.

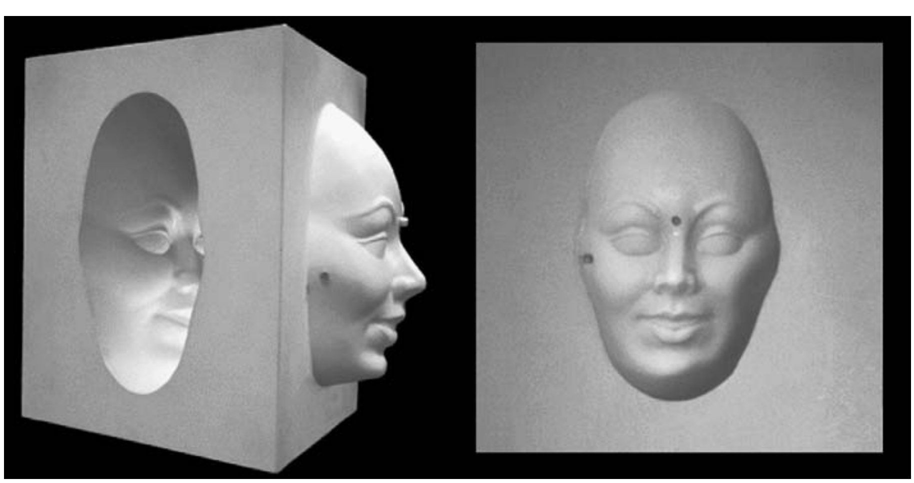

Fig. 1 – Left panel. The apparatus used to present the normal and hollow faces. Two small magnets, which served as targets, are shown in position on the forehead and cheek of the normal face. These targets were always presented separately. Right panel. The front view of the hollow mask. The lighting for this face comes from below, creating a shadow pattern that is similar to lighting from above for the normal faces. The reader should see this hollow mask as an illusory convex face.

In the first part of the experiment, there were 96 trials, 48 towards the illusory and 48 towards the normal face, 24 towards the cheek, and 24 towards the forehead. That is, there were 8 trials at each of the three distances for each target position. Participants were given 6 practice trials before beginning the experiment, 3 with the hollow (illusory) face and 3 with the normal face.

Deliberate pointing: Participants were instructed to point directly to the location where they perceived the target. On other trials, they were instructed to point the same corresponding distance below the face (to avoid the possibility of tactile feedback, particularly in the case of the normal face). These slow pointing movements were also recorded with the OPTO*TRAK*. In the first part of the experiment, there were 96 trials, 48 towards the display, and 48 below the display. The order of the testing conditions was randomized across participants. Within each condition, both viewing distance and face display were also randomized, with a different trial order for each participant. Because the responses made towards and below the display did not differ from one another, the results from both conditions were combined in subsequent analyses.

Paper-and-pencil drawing: After viewing the face for 3 s, participants drew the perceived position of the target on a piece of letter-sized paper by placing a mark to the right (for near) or left (for distant) of a vertical reference line representing the reference plate of the mask. A new piece of paper was presented on each trial, and participants drew the position of only one target on that piece of paper. In the first part of the experiment, participants were tested 24 times for each target position (cheek and forehead), i.e., 8 times at each of the three distances for the convex and concave mask in a different random order for each participant.

The perceptual measures of the perceived target distances (both drawing and deliberate pointing) were each performed in two separate blocks, half of the trials before and half after testing the fast flicking movement. This was done to test whether or not performing the visuomotor task would influence the way the target positions (and as a result, the illusory display) are perceived. As it turned out, this made no difference, so the results were collapsed.

In a final set of trial blocks, participants were tested on all three tasks with the hollow face looking hollow. Since only one type of display (the hollow mask) was presented, the number of trials was halved. In all other respects, the testing was identical.

3. Results

3.1. *Drawing*

As can be seen in Fig. 2, when participants drew the position of the target presented on the forehead or cheek of the different masks, they showed evidence of a robust hollow-face illusion ($F(2,14) = 57.4$, $P < 0.001$). In other words, the relative positions of the target on the illusory display were the same as they were on the normal face mask, although the distance between them was seen as slightly compressed (Fisher–Hayter, $P < 0.01$). The relative positions of the targets on the hollow face looking hollow were veridical, i.e., reversed with respect to the normal face (Fisher–Hayter, $P < 0.01$).

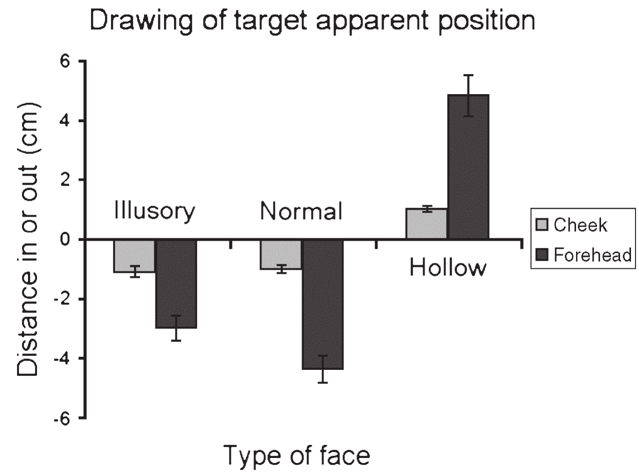

Fig. 2 – Perceptual estimates. Participants drew on a sheet of paper the perceived positions of the target on the foreheads and cheeks of the faces. The mean distances of the pencil marks (along the horizontal z axis) from the line indicating the reference plate are shown on the ordinate. Error bars indicate standard errors of the mean.

3.2. *Fast flicking*

Participants were equally fast at initiating their flicking movements to the illusory (504 ms, SE = 32 ms) and the normal face (507 ms, SE = 34 ms), suggesting that the presence of the illusion did not slow down the programming of the required movements. The movement onset time with the hollow face looking hollow was significantly faster (448 ms, SE = 31 ms; $F(2,14) = 8.3$, $P < 0.01$; Fisher–Hayter, $P < 0.01$), an improvement which probably reflects the absence of the de-focusing lens and the brighter viewing conditions on trials in which the hollow mask was seen as hollow (Jiang et al., 1991).

As Fig. 3 shows, in all three cases, the movements were directed to the real position of the targets on the cheek and forehead. Thus, the end points of the flicking movements to both the illusory (hollow) face and the hollow face looking hollow did not differ from each other but both differed significantly from the end points of the movements to the normal face ($F(2,14) = 139.6$, $P < 0.001$).

Indeed, the distance at which the target was flicked from the forehead of the normal face was more than 9 cm closer to the participants than the distance at which it was flicked from the forehead of either the hollow face looking hollow or the hollow face looking normal (the illusion). The flicking on both the normal face and the hollow face looking hollow corresponded to the seen positions within about a centimeter; but for the hollow face looking normal (illusion), the flicking for the forehead was about 7 cm behind its seen position. In other words, for the hollow-face illusion, the perceived position of the target went one way and the final position of the hand in the flicking task went the other. Finally, it should be noted that the flicking responses to the hollow-face illusion showed no evidence of improving over time ($F(11,77) = 0.86$; ns) and that participants failed to hit the target on about half the trials.

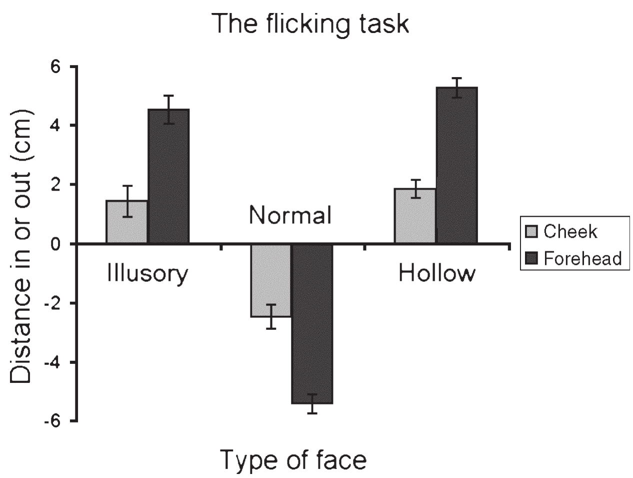

Fig. 3 – The flicking task: the mean distance of the hand (along the z axis) at the moment the participant attempted to flick off the target from the cheek or forehead of the normal or hollow mask. Notice that, in the case of the illusory face, the end points of the flicking movements corresponded to the actual distances of the targets, not to consciously seen distances (Fig. 2). Error bars indicate standard errors of the mean.

Fig. 4 shows that, early in the flicking movement, at the point of maximum velocity, the horizontal (z axis) distance covered on the way to the target was greater for both the hollow face looking hollow and the hollow-face illusion than it was for the normal face ($F(2,14) = 37.7$, $P < 0.001$ and Fisher–Hayter, $P < 0.01$).

It should be noted, however, that the distance reached on trials with the hollow face looking hollow was slightly greater than it was for the illusory face (Fisher–Hayter, $P < 0.05$), which again probably reflects the absence of the de-focusing lens and the brighter viewing conditions that were required to make the hollow face appear hollow (Jiang et al., 1991). But even in this condition, participants failed to hit the target on approximately 30% of the trials.

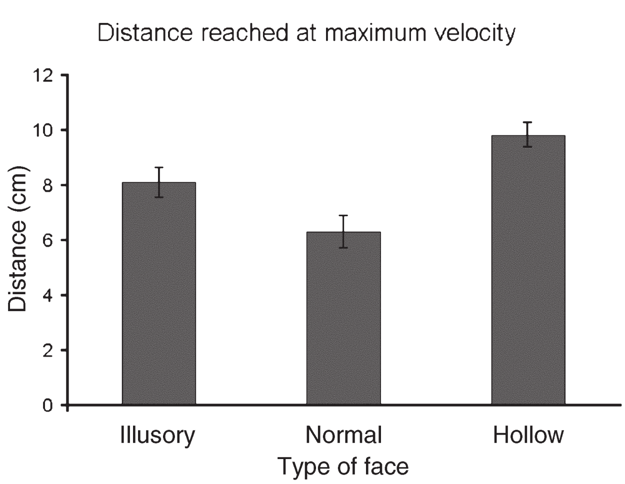

Fig. 4 – The mean distance (along the *z* axis) from the start button reached at maximum velocity for the flicking movements made to targets placed on the three different displays. When maximum velocity was reached, early in the movement trajectory, participants were already reaching out further for both the hollow faces, however they appeared, than they were for the normal face. Error bars indicate standard errors of the mean.

Fig. 5, which shows the paths of the flicking movements (seen from the side), also makes the point that participants were programming their responses differently for the normal and illusorily depth-reversed faces. Note that the trajectories for these two conditions separated right from the start of the movements. Indeed, the average trajectory for movements made to the illusory face was much more similar to the average trajectory for the hollow face looking hollow than it was to the average trajectory for the normal face.

3.3. Slow pointing

There were clear differences in the movement onset times for pointing with the three different displays ($F(2,14) = 7.4$, $P < 0.001$). The mean onset time for pointing movements to the illusory (hollow) face (737 ms, SE =63 ms) was significantly longer (Fisher–Hayter, $P < 0.05$) than the mean onset time for movements to the normal face (692 ms, SE = 53 ms), and both were significantly longer (Fisher–Hayter, $P < 0.01$) than the onset time for pointing movements to the hollow face looking hollow (612 ms, SE = 44 ms). Movement times did not differ across the three conditions. The average duration of the pointing movements (1660 ms, SE = 155 ms), however, was more than three times longer than the average duration of the flicking movements (471 ms; SE = 30 ms).

As Fig. 6 shows, the final positions of the pointing movements made to the illusory (hollow) face, like those made to the normal face, were in front of the reference plate. In contrast, the final positions of the pointing movements made to the hollow face looking hollow were located beyond the reference plate ($F(2,14) = 203$, $P < 0.0001$). The final positions of the pointing movements made to the illusory face were somewhat closer to the reference plate as compared to the final positions of movements made to the normal face (Fisher–Hayter, $P < 0.01$) and also did not reflect the perceived relative

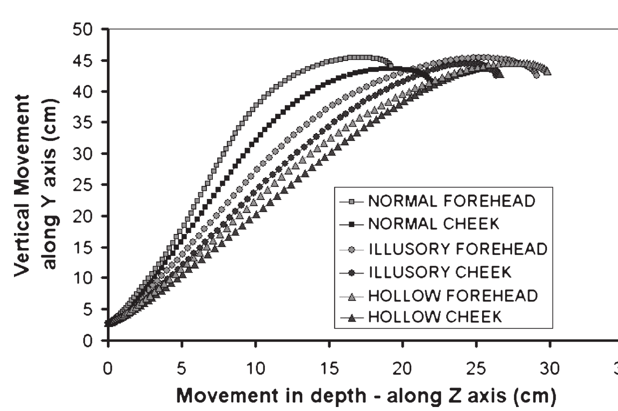

Fig. 5 – A side view of the paths of movements in the flicking task in the three conditions. The profiles show position of the moving finger in the *y* (vertical) and *z* (depth) axes. The IRED placed on the base of the index finger was tracked at 200 Hz (and the obtained data were then normalized). The mean distance of the reference plate of the display was 24.8 cm from the start button.

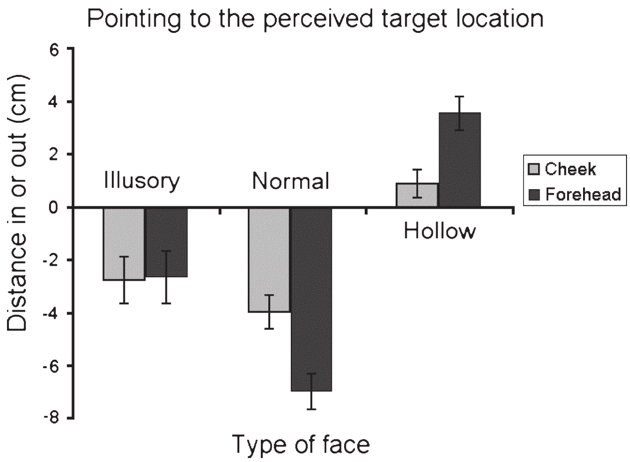

Fig. 6 – The pointing task: the mean final location of the finger with respect to the reference plate for pointing movements made to the cheek and forehead targets for all three displays. Notice that the movements made to all three displays tended to end near the perceived positions of the targets, although the movements to the targets on the illusory face did not distinguish between the cheek and forehead targets. Error bars indicate standard errors of the mean.

positions of the forehead and cheek targets. Nevertheless, as Fig. 7 illustrates, the pointing movements were typically directed to locations in front of the reference plate, in sharp contrast to the flicking movements, which were always directed at the real position of the targets deep inside the mask ($F(2,14) = 27.7$, $P < 0.001$).

3.4. *Effect of flicking on perceptual estimates*

Neither the drawing estimates nor the pointing movements were affected by prior performance of the flicking task ($F(1,7) = 0.3$, ns; and $F(1,7) = 1.6$, ns, respectively). In other words, there was no difference between the perceptual measures collected before the flicking task and the measures collected afterwards. This demonstrates that the haptic feedback from the veridical position of the target on flicking trials did not influence perception of the hollow-face illusion.

4. Discussion

The results of the experiment demonstrate that, despite the presence of a strong hollow-face illusion, participants directed rapid movements to the real, not the illusory positions of the targets. To do this, the visuomotor system must either have access to other sources of visual information or process the available information differently from that driving the illusion. Participants seem to be unaware of the veridical depth information they are using to control their flicking movements. Moreover, the use of this veridical depth information does not 'break' the illusion.

The analysis of the trajectories of the finger during target-directed flicking movements shows that these movements were 'programmed' using the real position of the target—even on trials in which the hollow-face illusion was present. In other words, the motor system was not initially fooled by the visual illusion, as participants did not move their hand to the perceived position of the target first, correcting their movement later. It is also apparent that the participants were not moving their finger "blindly" forward until they made physical contact with the mask. Instead, they appear to have programmed the distance to be moved quite early on. As a consequence, the trajectories for the two kinds of displays–illusory and normal–separated right from the start. In other words, it was not the perceived position of the target but its actual distance that determined the movement trajectory.

The results from the drawing test show that the illusory face was perceived as somewhat compressed. This effect, which has been reported by others (Hartung et al., 2005), may reflect the operation of Emmert's Law, in which the apparent size of the protruding features such as the forehead would appear smaller for the illusory than for the real face. In any case, the fact that the illusory face appeared somewhat compressed and that there were other cues, such as reverse motion parallax, meant that participants could have distinguished between the illusory and normal mask. In principle, then, the participants could have used this knowledge to make larger amplitude movements when presented with the illusory face. But this seems unlikely. First, the position of the display was randomly changed from trial to trial making it difficult to use this strategy. Second, they took no longer to initiate their flicking movement to the targets on the illusory display than they did to the targets on the normal face. In addition, there was no evidence that participants learned to increase the amplitude of their flicking movements to the illusory face as the experiment progressed. Finally, we have

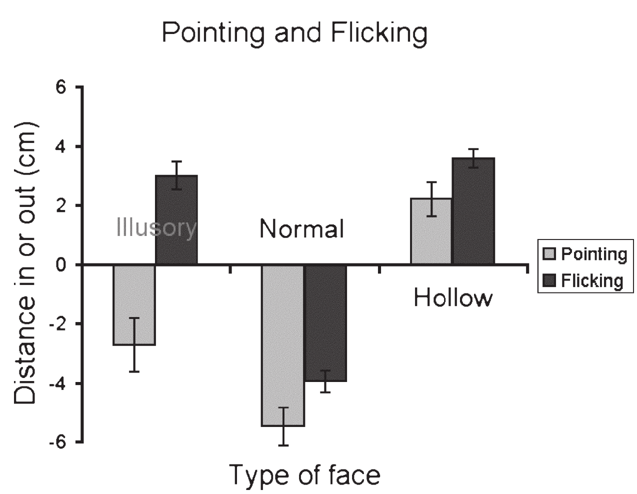

Fig. 7 – The slow pointing and fast flicking responses (the endpoints are averaged over both target positions). For the normal face and the hollow face looking hollow, both the flicking and slow hand movements were nearly veridical. For the hollow face looking convex (the illusory reversal of depth), the movements were very different. Here, the end points of the slow pointing corresponded to the illusory position of the target (*in front* of the reference plate) whereas the end points of the fast flicking movements corresponded to their actual position (*behind* the reference plate). Error bars indicate standard errors of the mean.

evidence from a study in progress (Króliczak, Heard, Goodale, and Gregory, in prep.) that, when participants view the displays monocularly, the end points of their flicking movements fall considerably short of the real position of the target on trials with the illusory face, although the participants knew that they were looking at an illusion. All of these suggest that the participants in the present experiment were using veridical cues to drive their accurate flicking movements. One cue that was certainly available is vergence, which has been shown to be the major source of information for reaching (Mon-Williams and Dijkerman, 1999). Moreover, there is evidence that transient shifts in vergence are mediated by a system that employs a single low-pass sensitive channel (Edwards et al., 1998), a system that would continue to operate when a de-focusing lens was placed over one eye.

The pronounced dissociation we found between perceptual report and rapid target-directed movements conflicts with the conclusion from an earlier study (Hartung et al., 2005), which used pointing as a visuomotor response. Given that pointing movements were directed to the perceived, not the real position of features on an illusory face, these authors concluded that the cues used by perceptual and visuomotor systems must be similar. We also found that, when participants pointed to the targets on the illusory face, they tended to point to the perceived, not the real position of those targets. But this is perhaps not surprising since, as we suggested earlier, there is evidence that pointing can often be influenced by cognitive factors (Bridgeman et al., 1997). This suggests that pointing and other more deliberate and slow movements do not have to engage the 'automatic' visuomotor mechanisms in the dorsal stream but instead can be mediated by 'perceptual' processing in the ventral stream (Rossetti et al., 2005). Indeed, although the movement times are not reported in the earlier study, the lack of difference between pointing and psychophysical measures (Hartung et al., 2005) may mean that their participants also adopted slow hand movements when pointing to the hollow-face illusion.

To conclude: the strong stable cognitive illusion of reversed depth did not substantially disturb rapid "flicking" behavior, which is a fast and simple goal-directed motor task. This demonstrates that visual information for perception and action can, under certain conditions, be dissociated. The visuomotor system can use bottom–up sensory inputs (e.g., vergence) to guide behavior to veridical locations of targets in the real world, even when perceived positions are influenced, or even reversed, by top–down processing. This fits the concept of two cortical streams of visual processing: one (more ancient) system for immediate rapid action, and the other, a more sophisticated representational system that supplements real-time signals with knowledge from the past to plan future behavior.

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