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Integration of structure-from-motion and symmetry during surface perception

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Sinusoidal motion of elements in a random-dot pattern can elicit a striking percept of a rotating volume, a phenomenon known as structure-from-motion (SFM). We demonstrate that if the dots defining the volume are 2D mirror-symmetric, novel 3D interpretations arise. In addition to the classical rotating cylinder, one can perceive mirror-symmetric, flexible surfaces bending along the path of movement. In three experiments, we measured the perceptual durations of the different interpretations in a voluntary control task. The results suggest that motion signals and symmetry signals are integrated during surface interpolation. Furthermore, the competition between the rotating cylinder percept and the symmetric surfaces percept is resolved at the level of surface perception rather than at the level of individual stimulus elements. Concluding, structure-from-motion is an interactive process that incorporates not only motion cues but also form cues. The neurofunctional implication of this is that surface interpolation is not fully completed in its designated neural “engine,” MT/V5, but rather in a higher tier area such as LOC, which receives input from MT/V5 and which is also involved in symmetry detection.

Keywords: 3D surface and shape perception, motion—2D, perceptual organization, structure-from-motion, surface interpolation, symmetry perception


Introduction

The principal task of the human visual system is to establish a 3D representation of the visual environment. To this end, it uses a plenitude of depth cues, for instance, ocular cues such as accommodation and binocular disparity, and pictorial cues such as linear perspective, shading, and texture gradients (e.g., Palmer, 1999; Todd, 2004).

Another important source for the extraction of structural 3D information is visual motion. Even in the absence of other depth cues, motion can convey rich information about object structure. In a particularly compelling illustration of this phenomenon, coined kinetic depth effect or structure-from-motion (SFM), sinusoidally moving dots evoke a strong percept of volumetric form (Braunstein, 1962; Green, 1961; Todd & Norman, 1991; Treue, Andersen, Ando, & Hildreth, 1995; Treue, Husain, & Andersen, 1991; Wallach & O’Connell, 1953; for a review, see Andersen & Bradley, 1998; see also Movie 1a). The present consensus on the functional implementation of SFM seems to be that, first, the local velocities of individual dots are integrated to derive a global velocity field. Second, mental representations of surfaces are constructed based on this velocity field and they are updated and refined across time (Andersen & Bradley, 1998; Hildreth, Grzywacz, Adelson, & Inada, 1990; Hol, Koene, & van Ee, 2003; Treue et al., 1995, 1991; Ullman, 1984).

Neurofunctional research attempted to pinpoint the neural correlates of SFM. Bradley, Chang, and Andersen (1998) presented evidence from monkey research suggesting MT/V5 as the neural analog of surface interpolation. They showed that, in a bistable rotating cylinder stimulus, the activity of MT/V5 triggered by moving elements is higher when these elements are perceived as being part of the front surface rather than part of the back surface. MT/V5 was also shown to be sensitive to speed gradients, to encode the orientation of surfaces tilted in depth, and to be affected by attention to motion-defined surfaces, with similar results for humans and monkeys (Martinez-Trujillo et al., 2005; Orban, Sunaert, Todd, van Hecke, & Marchal, 1999; Treue & Andersen, 1996; Vanduffel et al., 2002; Wannig, Rodriguez, & Freiwald, 2007; Xiao, Marcar, Raiguel, & Orban, 1997). Nonetheless, there is no stringent evidence requiring that the computation of surfaces is also fully completed in this area. In fact, the involvement in SFM of a number of other cortical areas such as V3A and the lateral occipital complex (LOC) suggests that SFM is supported by a widespread cortical network (Brouwer & van Ee, 2007; Orban et al., 1999; Paradis et al., 2000; Vanduffel et al., 2002).

Many of these areas are involved not only in motion processing but also in the processing of static form. For
instance, Murray, Olshausen, and Woods (2003) showed that part of the LOC is activated both by SFM stimuli and by 3D line drawings. Using simultaneous EEG and MEG recordings, Jiang et al. (2008) revealed subsequent activations of MT, LOC, and ventral temporal regions to motion-defined 3D shapes. Most importantly, activity in LOC was associated with induced gamma synchronization, a hallmark of perceptual binding.

Despite the remarkable overlap between brain regions involved in SFM and form processing (for a review, see Kourtzi, Krekelberg, & van Wezel, 2008), there have been no complementary reports in the psychophysical literature demonstrating that the computation of motion-defined surfaces is affected by form cues. On the contrary, it has been argued that the spatial structure of dots defining, for instance, a rotating cylinder does not affect surface interpolation (Li & Kingdom, 2001; Treue et al., 1991).

In this article, we show that structure-from-motion and symmetry are integrated during surface perception, and that this interaction entails novel 3D interpretations. The starting point for this study was an informal observation by the first author, which was further substantiated during a pilot experiment with sixteen naive participants. If the parallel projection of dots attached to a rotating cylinder yields a random-dot pattern in 2D, the classical interpretations are perceived, that is, a clockwise or counterclockwise rotating cylinder (Hol et al., 2003) or two convex or concave surfaces (Chen & He, 2004) are perceived. If, however, the parallel projection yields a pattern that is mirror-symmetric about the vertical midline in 2D, a number of additional 3D interpretations arise, which have not been covered in the literature yet (Figure 1 and Movie 1b). All novel interpretations have in common that one usually perceives two moving surfaces that are mirror-symmetric about a symmetry plane whose 2D projection coincides with the vertical midline. In contrast to the rigid rotating cylinder percept, these surfaces are flexible and they bend along the perceived path of movement. Participants did not report these percepts when exposed to random-dot stimuli, suggesting that the perception of symmetric surfaces is linked to the symmetry of the stimulus.

The novel interpretations can be roughly classified according to two characteristics. First, the symmetric surfaces can be perceived as either colliding at the vertical midline and then bouncing off in the opposite direction (colliding surfaces), or as crossing by each other at the vertical midline without any physical contact (crossing surfaces). Second, motion can be cyclic, in which case each surface returns to its perceived 3D position within one cycle of sinusoidal motion, or winding, in which case the surfaces are perceived to wind forward or backward, resembling the movement of a snake (Figure 2).

The preponderance of perceptual interpretations that are given by a conjunction of motion and symmetry (for convenience, we will use the term symmetry to refer to mirror symmetry) pleads for an integration of motion
Figure 1. Perceptual interpretations of the symmetric motion pattern. (a) Schematic display of the physical stimulus, consisting of a dot pattern that is symmetric about the vertical midline. For simplicity, only 8 dots are depicted. As indicated by the white arrows, symmetric dots move in opposite directions with the same velocity so that symmetry is preserved through time. (b) Classical 3D interpretations, a clockwise or counterclockwise rotating cylinder. (c) Novel 3D interpretations, two (or more) symmetric surfaces. At the vertical midline, symmetric elements meet and they can be perceived as crossing by each other without physical contact (crossing surfaces) or as colliding and then bouncing off each other in the opposite direction (colliding surfaces).

Figure 2. For each type of symmetric percept, there is a number of possible interpretations of the motion direction. In the schematic examples given here, motion is either cyclic (top row) or winding (bottom row). Movement is sketched from a top-down perspective, with the observer looking from below. Only one cycle is shown for each type of motion; the type of motion keeps repeating upon subsequent cycles. (a) Two possible interpretations of motion direction for the crossing surfaces percept. One surface is depicted as black, the other as gray. In the top view, both surfaces rotate continuously about the midpoint in opposite directions. In the bottom view, the surfaces wind forward toward the observer, crossing by each other without perceived physical contact. (b) Two possible interpretations of motion direction for the colliding surfaces percept. In the top view, cyclic motion is shown, with symmetric surfaces moving toward the observer (black arrows), then colliding, reversing direction, and moving back in the other direction (gray arrows). In the bottom view, symmetric surfaces move toward the observer (black arrows), collide, and then move on in the same direction (gray arrows) and keep moving forward. It is also possible to perceive motion in the opposite direction (i.e., surfaces receding from the observer).
signals and symmetry signals during surface interpolation. To establish the role of symmetry in the new interpretations, we conducted Experiment 1 wherein we presented only symmetric SFM stimuli. Participants were asked to attempt to perceive either a rotating cylinder or symmetric surfaces, and we measured the perceptual durations of these two interpretations as a function of a number of viewing conditions.

To our knowledge, this is the first empirical study linking symmetry processing and SFM. It is only in computer vision that this link has received some attention. There, symmetry was shown to boost the efficiency of SFM algorithms (Mitsumoto, Tamura, Okazaki, Kajimi, & Fukui, 1992; Poggio & Vetter, 1992; Rothwell, Forsyth, Zisserman, & Mundy, 1993; Zabrodsky & Weinshall, 1997).

Experiment 1

Experiment 1 was conducted to substantiate the claim that symmetry processing is involved in the perception of symmetric surfaces. The starting point was the fact that motion processing and symmetry processing have different signatures in terms of eye movements. To be more clear, the efficacy of symmetry detection peaks when the symmetry axis is foveated and it has been shown to drop with increasing eccentricity of the symmetry axis, at least for static stimuli (e.g., Gurnsey, Herbert, & Kenemy, 1998; Herbert & Humphrey, 1993; Saarinen, 1988). In contrast, for the rotating cylinder percept, Hol et al. (2003) showed that perceptual duration is not affected by viewing condition. Consequently, if symmetry processing is involved in the perception of symmetric surfaces, foveation of the symmetry axis should enhance the perceptual duration of the symmetric surfaces percept. To test this, we introduced four viewing conditions, namely central fixation, bottom fixation (below the stimulus but still on the symmetry axis), left fixation, and a free viewing condition. Considering the free viewing condition, we expected that participants focus on the symmetry axis if they were cued to perceive the symmetric surfaces but not if they were cued to perceive the rotating cylinder.

Methods

Apparatus

We used a Tobii 1750 integrated eye tracker to display stimuli and to register eye movements concurrently. The refresh rate of the 17\" screen amounted to 75 Hz and the resolution was 1280 × 1024 px². The sampling rate of the eye tracker was 50 Hz. Viewing distance was about 67 cm. Although Tobii is quite robust to head movements within a certain range, participants were asked to move their head as little as possible throughout the experiment. Participants’ button responses were recorded using a button box with a 1-ms temporal accuracy. Stimulus presentation and data acquisition were performed using Neurobehavioral Systems Presentation. This software was complemented by Tobii’s eye tracking software and a Presentation interface.

Participants

Sixteen right-handed undergraduate students participated in this experiment. All participants were naive with respect to the purpose of the experiment and they had normal or corrected-to-normal vision. None of them had participated in the pilot experiment.

Stimuli

Parallel projections of dots on a rotating cylinder were used as stimuli. Each stimulus consisted of 48 elements that were uniformly distributed on the cylinder surface and that moved according to a sinusoidal velocity function. During the pilot phase, this number of elements proved most promising in evoking both the rotating cylinder percept and the novel percepts reliably. All elements were symmetric about the vertical midline of the stimulus. To produce 2D symmetry starting from the cylinder, half of the elements were randomly placed on one half of the cylinder. Subsequently, this half was copied and shifted onto the other half, resulting in the 2D projection being symmetric. In 2D, the two elements in each symmetry pair had equal-magnitude, opposite-sign movement vectors, so that perfect bilateral symmetry was preserved through time.

We also took care of an uncontrolled variable that we became aware of during the pilot experiment. Participants reported that, on some occasions, they perceived four or even six symmetric surfaces. Apparently, clusters of elements were grouped on the basis of the relative proximity of the elements on the cylinder surface. We will address a possible implication of this finding in the General discussion section. For the experiments at hand, it was more important to keep this factor under control. Therefore, we imposed a spatial contiguity constraint on the stimulus. This means that, during stimulus generation, the first element was placed randomly on the cylinder surface; each subsequent element was also placed randomly, but it was constrained to be within the vicinity (80 px) of at least one previously placed element. This method assured that, in the symmetric interpretations, the number of perceived surfaces was always two.

Dot diameter was 10 px or about 0.22° of visual angle. The placement of the elements was limited to a window of 400 × 400 px² or 8.9° × 8.8° of visual angle. The actual height of a stimulus could be lower than 400 px since elements were randomly placed. Angular velocity was 90°/s and element positions were updated in every frame.
All elements were white and the color of the background was set to mean gray value. All stimuli were randomly generated during the experiment and each stimulus was centered on the screen. Movie 2 gives a sample stimulus.

**Procedure**

Our aim was to measure perceptual durations of the rotating cylinder percept and the symmetric surfaces percept as a function of exogenous (stimulus characteristics) and endogenous (voluntary control, eye movements) parameters. For classical SFM percepts, it was shown earlier that perceptual switches are subject to voluntary control, but only within certain limits imposed by stimulus and task parameters (Brouwer & van Ee, 2006; Hol et al., 2003; Klink et al., 2008; Raemaekers, van der Schaaf, van Ee, & van Wezel, 2009). To measure perceptual durations, we adopted the procedure used in Hol et al.’s (2003) study on the effects of attention on SFM. The procedure was given as follows.

Each trial was initiated via a button press. Subsequently, a cue was presented, indicating which kind of interpretation, the rotating cylinder or the symmetric surfaces, participants should attempt to perceive. The physical stimulus was always symmetric, irrespective of which percept was cued. Upon another button press, a fixation dot appeared and remained on the screen until the end of the trial. Participants had to fixate this dot. After 1 s, the stimulus appeared and remained on the screen for 20 s. The task of the participants was to press the left button as soon as they clearly perceived the cued percept and to press the right button when the percept switched to the other stimulus class, when it became ambiguous, or when depth was not perceived any more. Participants were told that the exact type of movement (clockwise or counter-clockwise rotation in case of the rotating cylinder percept, and cyclic or winding motion in case of the symmetric surfaces percept) was irrelevant and that they should also ignore perceived switches of movement direction.

To test the effects of eye movements, we introduced four viewing conditions. First, central fixation, wherein a fixation dot was presented in the center of the stimulus, on the symmetry axis. Second, bottom fixation, wherein the fixation dot was presented 10 px below the stimulus, however still aligned with the symmetry axis; since stimulus height varied due to the random placement of dots, the absolute distance between the fixation dot and the center of the stimulus necessarily also varied in the bottom fixation condition. Third, left fixation, wherein the fixation dot was presented 100 px to the left of the center, which is halfway between the symmetry axis and the left border of the stimulus. Finally, free viewing, wherein there was no fixation dot.

In the first three viewing conditions, participants were told to strictly fixate the fixation dot. In the free viewing condition, eye movements were unrestricted; participants were instructed, however, to try to move their eyes in such a way that the cued percept could be best perceived. The same kind of symmetric dot pattern was presented in each trial, irrespective of which percept was cued.

Each experiment was preceded by a demonstration, wherein a number of sample stimuli were shown and the possible percepts were explained. All participants were able to perceive the different interpretations. Usually, the rotating cylinder interpretation was perceived first. When instructed to focus on the symmetry axis, participants could readily perceive the symmetric surfaces interpretation. After the demonstration, they completed a practice phase, with one practice trial given for each of the eight subconditions in a random order. This was followed by the experimental phase.

We used two different kinds of cues, one for the rotating cylinder and one for the symmetric surfaces. Likewise, in order to record eye movements, the eye tracker was calibrated before the start of the experiment. The total number of trials amounted to 2 [percept conditions] × 4 [viewing conditions] × 8 [measurements] = 64. The order of trials was randomized.

**Dependent variable**

To measure the perceptual salience of the different percepts, we used perceptual duration as a dependent variable, as specified in Hol et al. (2003). Perceptual duration refers to the total amount of time the cued interpretation is perceived within a trial. Since each
stimulus was presented for 20 s, duration was bracketed between 0 s (when the cued interpretation was not perceived at all) and 20 s (when the cued interpretation was perceived all the time). Note that Hol et al. also introduced reaction time, defined as the first point in time wherein the cued interpretation is perceived, as a second dependent measure, which is not considered here. In our opinion, it does not add substantial information because it is negatively correlated with perceptual duration, at least for long perceptual durations. We verified this negative correlation by rerunning our analyses for reaction time, and as expected, we found opposite patterns of results for perceptual duration and for reaction time (i.e., long perceptual durations corresponded to short reaction times, and vice versa).

Results
Perceptual durations

We investigated the perceptual durations using a $2 \times 4$ (Percept × Viewing Condition) repeated measures ANOVA. The results are depicted in Figure 3a. Overall, the rotating cylinder was perceived more often than the symmetric surfaces (Percept; $F(1,15) = 44.289, p < 0.001$). There was no main effect of Viewing Condition ($p = 0.619$), but there was a significant interaction between Percept and Viewing Condition, $F(3,45) = 13.89, p < 0.001$. Using post-hoc tests, perceptual durations for the rotating cylinder percept and the symmetric surfaces percept were analyzed separately. A Bonferroni-corrected $\alpha$-value of 0.05 / 6 = 0.0083 was used.

For the rotating cylinder percept, there was no significant difference in perceptual duration between central fixation and bottom fixation ($p = 0.487$), and also no difference between left fixation and free viewing ($p = 0.535$) in terms of perceptual duration. However, there was a significant difference between these two pairs of conditions ($p < 0.001$). In other words, the rotating cylinder percept was more persistent when fixation was off the symmetry axis (left fixation) or when participants viewed freely than when participants had to fixate the symmetry axis (central fixation and bottom fixation).

The opposite pattern of results was found for the symmetric surfaces condition. Again, there was no significant difference between central fixation and bottom fixation ($p = 0.762$), and no difference between the left fixation and free viewing ($p = 0.756$). Again, there was a significant difference between these two pairs of conditions ($p < 0.001$), but this time, the difference was in the opposite direction.

To investigate whether voluntary control of the perceptual interpretation gets more effective with time, we fitted a regression line through the perceptual durations as a function of trial number. As depicted in Figure 4b, the analysis reveals a positive trend, albeit small. The slope for the rotating cylinder percept was positive (15.88 ms/trial) but not significantly different from zero ($p = 0.232$), and likewise for the symmetric surfaces percept (24.85 ms/trial; $p = 0.084$).

Eye movements

We examined the fixation conditions and the free viewing condition separately. In all fixation conditions, mean eye position was within one standard deviation of the corresponding fixation dot position. In paired-samples $t$-tests conducted for $x$ and $y$ dimensions separately, we did not find any significant differences between the conditions in terms of means (all $p$ values > 0.101) and standard deviations (all $p$ values > 0.104) of the fixation data.

We also investigated whether there was a difference in terms of the number of saccades between the three fixation conditions. To estimate the number of saccades from the raw data, we applied a spatiotemporal fixation filter consisting of two sliding averaging windows. As Figure 4a illustrates, participants made slightly less than one saccade per trial on average. A repeated measures ANOVA did not show any systematic relationship between number of saccades and experimental condition (all $p$ values > 0.424), suggesting that participants were fixating equally well in all fixation conditions.

For the free viewing conditions, we were interested in whether there was a qualitative difference in terms of eye movements between the rotating cylinder condition and the symmetric surfaces condition. Figures 4c and 4d gives eye movement traces for the rotating cylinder and the symmetric surfaces conditions. The plots suggest that participants performed rather horizontal eye movements.

![Figure 3](image-url)
and fixations off the symmetry axis in the rotating cylinder condition but tried to stick to the symmetry axis in the symmetric surfaces condition. To quantify this, we calculated the aspect ratio for the rotating cylinder and symmetric surfaces conditions, that is, the extent of the eye movements along the \( x \) dimension (width) divided by the extent of the eye movements along the \( y \) dimension (height). To this end, we used the standard deviations along each dimension (an alternative would be to take the minimum and maximum values along the \( x \) and \( y \) dimensions, but these values are more susceptible to outliers than the standard deviation). Figure 4b depicts the aspect ratio for the rotating cylinder and symmetric surfaces conditions. A paired-samples \( t \)-test revealed that the aspect ratio is indeed different between these two conditions, \( t(15) = 2.404, p < 0.05 \).

Discussion

Both the rotating cylinder and the symmetric surfaces could be perceived under all viewing conditions, but we found different effects of viewing condition on the perceptual durations of the two percepts (Figure 3a).

For the symmetric surfaces percept, perceptual duration is highest for central fixation and bottom fixation. In other words, efficient perception of the symmetric surfaces requires foveation of the symmetry axis, which suggests that symmetry processing is involved in the perception of symmetric surfaces (see Gurnsey et al., 1998; Herbert & Humphrey, 1993; Saarinen, 1988).

For the rotating cylinder percept, the opposite pattern of results was found. In contrast to Hol et al. (2003), who used similar viewing conditions and who did not find an effect of viewing condition on perceptual duration, we found that it is higher for free viewing and left fixation than when the symmetry axis is fixated. This pattern of results suggests that there is a direct perceptual competition between the rotating cylinder interpretation and the symmetric surfaces interpretation. Furthermore, the fact that, for each fixation condition, the perceptual duration for the rotating cylinder percept and the symmetric surfaces percept adds up to more than 20 s suggests that voluntary control is involved in the perception of these stimuli, as proposed in other studies on SFM (Brouwer & van Ee, 2006; Hol et al., 2003; Klink et al., 2008). This is in line with the first author’s own observations and some informal reports by participants. We analyzed whether voluntary control improves with time and we found a small positive trend for both percepts (Figure 3b), but it was not significant in either case.

In terms of eye movements, we found that participants made slightly less than one saccade per trial (Figure 4a). This is less than Brouwer and van Ee (2006) reported using a different paradigm (about 10 saccades/min), but it is roughly in the same order of magnitude. Comparing the aspect ratios in the free viewing condition, we found that participants perform relatively more horizontal (potentially smooth pursuit) eye movements when they try to perceive the rotating cylinder than when they try to perceive symmetric surfaces (Figure 4b). This suggests that smooth pursuit might have been involved in the perception of the rotating cylinder but not in the perception of symmetric surfaces. The temporal resolution of our eye tracker is too low for a comprehensive analysis of smooth pursuit eye movements, but Brouwer and van Ee (2006) already presented evidence that voluntary control of a bistable rotating sphere is improved with smooth pursuit.
To sum up, first, foveation of the symmetry axis enhances perceptual durations of the symmetric surfaces percept, suggesting that symmetry signals are integrated during SFM processing. Second, we found evidence that the rotating cylinder percept and the symmetric surfaces percept engage in perceptual competition, and showed that voluntary control seems to be involved in resolving this competition. In the SFM literature, it is proposed that the surface level is crucial to perceptual competition (e.g., Brouwer & van Ee, 2006; Hol et al., 2003; Klink et al., 2008; Treue et al., 1995, 1991). Furthermore, there is evidence that, in bistable stimuli, surfaces can be the target of visual attention (Wannig et al., 2007). In light of this, perceptual competition between the different interpretations is most probably resolved at the level of surface perception.

A control experiment, reported next, served to corroborate the idea that the symmetric surfaces percept stems from an interaction between SFM processing and symmetry processing.

**Experiment 2**

In the stimuli used in Experiment 1, symmetry was defined by perfect point-to-point correspondences between individual dots. Consequently, the dots of each symmetry pair met at the symmetry axis, where net motion (i.e., the sum of motion vectors) amounted to zero. Qian, Andersen, and Adelson (1994) advocated that this kind of motion balance affects motion transparency (i.e., the perception of multiple transparent moving surfaces, a prerequisite for perceiving a rotating cylinder). They presented stimuli consisting of pairs of horizontally moving dots, whereby the dots in each pair had opposite motion vectors. Motion transparency was drastically reduced when the dots in each pair were vertically aligned, that is, when local net motion amounted to zero. To rule out that this motion balance (rather than symmetry processing) underlies the symmetric surfaces percept, we performed a control experiment using also symmetric stimuli whereby motion is not balanced. The rationale was that, if motion balance underlies the symmetric surfaces percept, no symmetric surfaces would be perceived with unbalanced symmetric stimuli.

To create unbalanced symmetric stimuli, we exploited the well-documented fact that symmetry detection is quite robust to various kinds of distortions, such as the addition of noise dots, spatial jittering of symmetry dots, or phase randomization in the frequency domain (see, e.g., Barlow & Reeves, 1979; Dakin & Herbert, 1998; Rainville & Kingdom, 2002; Wagemans, van Gool, Swinnen, & van Horebeek, 1993). As explicated in the method, a manipulation similar to spatial jitter was applied to remove motion balance but still preserve symmetry on a rough spatial scale.

To further corroborate the importance of the interpolated surfaces, rather than explicit point-to-point correspondences, in the perception of symmetric surfaces, we also added a limited-lifetime condition whereby dot pairs were constantly replaced by new randomly placed dot pairs.

**Methods**

**Apparatus**

Stimuli were displayed on a 19" monitor at a refresh rate of 100 Hz. Viewing distance was 60 cm and a chinrest was used to restrict head movements. The resolution of the screen was $1280 \times 1024$ px$^2$.

**Participants**

Twenty-two right-handed undergraduate students participated in this experiment. All participants were naive with respect to the purpose of the experiment and they had normal or corrected-to-normal vision. None of the participants had participated in the previous experiment or in the pilot experiment.

**Stimuli**

Stimulus parameters were largely identical to the stimulus parameters used in Experiment 1, except for the following. In Experiment 2, our stimuli featured element symmetries and surface symmetries. Element symmetries were identical to the stimuli used in Experiment 1, that is, random dots reflected about the vertical midline, with point-to-point correspondences and, hence, motion balance being preserved. Movie 3a gives a sample stimulus. To create surface symmetries, a spatial jitter manipulation was applied. First, a perfectly symmetric dot pattern was generated. With an unconstrained spatial jitter manipulation, dots could fall out of the boundaries of the original symmetric surfaces. To prevent this, we calculated the convex hull as an approximation of the surface border. The convex hull is the smallest subset of dots of the cluster, which, when connected by straight lines, encloses the whole cluster. Then, the dots were randomly shuffled, but only within the borders of the specified surface. By this, the dots were not symmetric any more but the two surfaces they specified were still symmetric on a rough spatial scale. Movie 3b gives a sample stimulus. In two additional conditions, we applied element symmetry and surface symmetry to stimuli with limited-lifetime dots. In these stimuli, elements disappeared after 120 ms and were instantly replotted at new, randomly chosen locations within the convex hull. To maintain perfect element symmetry, symmetric elements were removed and replotted pairwise. For surface symmetries, elements were also replotted pairwise, but the elements of each pair were not symmetric about the vertical midline. Movies 3c and 3d give sample stimuli for element symmetry and surface symmetry with limited-lifetime dots. In all conditions, dot
diameter was 10 px, which amounted to about 0.25° of visual angle. The stimulus was constrained to a \(400 \times 400\) px\(^2\) window (10.27° \times 9.86° of visual angle).

To substantiate the claim that surface symmetry contains 2D symmetry information at a rough spatial scale, we performed a multi-scale symmetry analysis based on Barlow and Reeves’ (1979) symmetry detection algorithm. The results, depicted in Figure 5, show that surface symmetry contains substantial 2D symmetry information, especially at lower spatial scales. Note that simultaneous

Movie 3. Sample stimuli used in Experiment 2. Each movie represents one of the four stimulus conditions. Note that, for the sake of comparability, all stimuli are based on the same surfaces. (a) Element symmetry. This stimulus is identical in its parameters to the stimuli used in Experiment 1. (b) Surface symmetry. Here, the dots are not symmetric with respect to each other, but the two dot clouds yield roughly symmetric surfaces. (c) Element symmetry with limited-lifetime dots. At each moment in time, the display is perfectly symmetric, but elements are constantly being replaced within the boundaries of the pre-specified symmetric regions. One can readily perceive symmetric surfaces. (d) Surface symmetry with limited-lifetime dots. At every moment in time, the display is not symmetric on a dot level, but yet, surface symmetry is easily perceived.
processing of symmetry at multiple spatial scales has been demonstrated in humans (e.g., Julesz & Chang, 1979; Rainville & Kingdom, 1999, 2002).

Procedure

The procedure was largely identical to the procedure used in Experiment 1. Participants completed 2 [percept conditions] × 4 [pattern types] × 9 [measurements] = 72 trials and the order of trials was again randomized.

Results

Again, we subjected perceptual durations to a repeated measures ANOVA. The results are depicted in Figure 6. There were significant effects of both Percept and Pattern Type, $F(1,21) = 5.228$, $p < 0.05$, and $F(3,63) = 3.374$, $p < 0.05$, respectively. Interaction was highly significant, $F(3,63) = 44.997$, $p < 0.001$. Using post-hoc tests, perceptual durations for the rotating cylinder percept and the symmetric surfaces percept were analyzed separately. A Bonferroni-corrected $\alpha$-value of $0.05 / 6 = 0.0083$ was applied. For the symmetric surfaces percept, we found that perceptual duration is higher for element symmetry than for surface symmetry, for both unlimited-lifetime dots ($p < 0.001$) and for limited-lifetime dots ($p < 0.001$). Furthermore, perceptual duration was longer than in the unlimited-lifetime condition, for both element symmetry ($p < 0.001$) and surface symmetry ($p < 0.001$). The exactly reverse pattern of results was obtained for the rotating cylinder, with all differences being significant.

Figure 5. Multi-scale analysis of symmetry for two sample stimuli, (top row) a random-dot pattern yielding the classical rotating cylinder percept and (bottom row) a surface symmetry. Symmetry was extracted from static frames for each of the 360 angular positions of the stimulus, depicted along the $x$-axis, and for ten different spatial scales, depicted along the $y$-axis. Based on Barlow and Reeves’ (1979) symmetry detection algorithm, the image was subdivided into $S \times S$ square-shaped bins for each value $S$ of spatial scale, and the numbers of elements contained in each bin were counted. The amount of symmetry was then operationalized as the normalized cross-correlation between the bins on the left and the right stimulus halves for each frame $\times$ spatial scale combination. The corresponding cross-correlations are depicted in color-coded form, with high correlation signifying high amounts of symmetry. Due to the random placement of dots, spurious symmetry is always present in random-dot patterns (red and orange spots), especially at low spatial scales. Although the surface symmetry lacks fine-grained symmetry information, it features high correlations throughout the motion cycle (i.e., at virtually all angular positions) on a rough scale, and symmetry information also extends into higher spatial scales than in the random-dot pattern. Mean cross-correlations were determined for 100 random-dot stimuli and 100 surface symmetries. An independent samples $t$-test showed that there is significantly more symmetry information in surface symmetries than in random-dot patterns ($p < 0.00001$).
The results show that explicit point-to-point correspondences are not required for perceiving symmetric surfaces. In line with the fact that symmetry is perfect in the element symmetry condition and "noisy" in the surface symmetry condition, we found that perceptual durations of the symmetric surfaces are longer for the former type of stimulus than for the latter. Again, this evidence pleads for the genuine involvement of symmetry processing in the perceptual construction of surfaces.

Additionally, we found that symmetric surfaces can be perceived with limited-lifetime dots. Moreover, perceptual durations of the symmetric surfaces are higher with limited-lifetime dots than with unlimited-lifetime dots. The latter finding could be due to the fact that the effective (or perceived) dot density is higher when dots are constantly replotted. This results in a more accurate and, therefore, more symmetric representation of the surface than with unlimited-lifetime dots. Alternatively, the increase in perceptual durations might also be due to impoverished motion signals with limited-lifetime dots, decreasing the dominance of the rotating cylinder percept and, thereby, increasing perceptual duration of the symmetric surfaces percept. However, we doubt that this alternative argumentation can fully explain the results at hand. First of all, the presentation duration of the dots (120 ms) was clearly above point-lifetime threshold (50–85 ms; Treue et al., 1991), so that one would not expect depth-from-motion analysis to be seriously obstructed by this manipulation. Second, effective dot density is higher with limited-lifetime stimuli than with unlimited-lifetime stimuli, which should support rather than hamper 3D perception. Third, participants were firmly instructed to respond only to surfaces moving in 3D, not to the percept of a 2D symmetric pattern, so that a decrease in the quality of depth perception should have decreased perceptual durations for both kinds of interpretations.

Another observation made in this experiment is that colliding surfaces are not perceived in the surface symmetry condition, although they can be perceived in the element symmetry conditions. While this might not be surprising, it seems reasonable to assume that it is the ambiguity introduced by the mutual occlusion of symmetric dots at the symmetry axis in the element symmetry condition. Once being occluded, it is ambiguous as to which element is which. If this kind of identity ambiguity is indeed responsible for the colliding surfaces percept, "labeling" the elements should affect which of interpretations is perceived. This issue was addressed in the next experiment.

**Experiment 3**

In this experiment, we investigated whether it is the ambiguity caused by the mutual occlusion of dots meeting at the symmetry axes that is responsible for the fact that both crossing surfaces and colliding surfaces can be perceived with the same stimulus. To resolve this ambiguity, we "labeled" elements by using both circles and triangles as element shapes. For the rotating cylinder, Li and Kingdom (1998, 1999, 2001) already showed that the visual system is sensitive to the "labeling" of elements by means of unique features such as orientation, luminance polarity, and spatial frequency.

**Methods**

**Apparatus**

The same apparatus was used as in Experiment 2.

**Participants**

Seventeen right-handed undergraduate students participated in this experiment. All participants were naive with respect to the purpose of the experiment and they had normal or corrected-to-normal vision. None of the...
participants had participated in the previous experiments or in the pilot experiment.

**Stimuli**

Stimulus parameters were largely identical to the stimulus parameters used in Experiment 2, except for the following. Now, stimulus elements consisted of circles and triangles. Circle diameter and triangle height and width were 13 px (about 0.33° of visual angle); the elements were slightly larger than in Experiments 1 and 2 to make circles and triangles more distinguishable. The discriminability of the two kinds of elements was informally verified during the demonstration of the stimulus.

In each stimulus, half of the elements consisted of circles and the other half consisted of triangles. To vary the amount of ambiguity, we introduced three shape pairing conditions. Figure 7 gives a schematic overview of these conditions. In the matched pairs condition, the two elements in each symmetry pair had identical shapes. By this, identity ambiguity was preserved so that this condition functioned as a baseline condition. In the unmatched pairs condition, each symmetry pair consisted of one triangle and one circle. In the swapping pairs condition, the elements of each symmetry pair also had different shapes. However, when crossing the midline, the elements swapped shapes. In the unmatched pairs condition and in the swapping pairs condition, identity ambiguity is resolved. More specifically, the unmatched pairs condition yields a stimulus that is compatible with the crossing surfaces interpretation but incompatible with the colliding surfaces interpretation. In contrast, the swapping pairs condition yields a stimulus that is not compatible with the crossing surfaces interpretation but that is compatible with the colliding surfaces interpretation.

**Procedure**

The procedure was largely identical to the procedure used in Experiment 1. In Experiment 3, we also investigated the rotating cylinder percept and the symmetric surfaces percept, but the symmetric surfaces cue was split into a colliding surfaces cue and a crossing surfaces cue (see Figure 1c), so that there were three different cues in
total. Participants completed 3 [percept conditions] × 3 [element shape conditions] × 8 [measurements] = 72 trials.

Results

We subjected perceptual durations to a 3 × 3 (percept × element shape) repeated measures ANOVA. The results are depicted in Figure 8. There were significant effects of both Percept and Element Shape, $F(2,32) = 42.447$, $p < 0.001$, and $F(2,32) = 8.934$, $p < 0.01$, respectively. Interaction was also significant, $F(4,64) = 16.061$, $p < 0.001$. Using post-hoc tests, perceptual durations were analyzed separately for the three different percepts. A Bonferroni-corrected $\alpha$-value of 0.05 / 9 = 0.0056 was applied.

For the rotating cylinder, perceptual duration was higher for unmatched pairs than for matched pairs ($p < 0.05$) or swapping pairs ($p < 0.05$), but this was not significant under the modified $\alpha$-value. There was no significant difference between the latter two conditions ($p = 0.767$). For the crossing surfaces percept, matched pairs tended to produce a higher perceptual duration than both unmatched pairs ($p = 0.076$) and swapping pairs ($p = 0.066$), but these effects were also not significant. Similarly, for the colliding surfaces percept, perceptual duration was higher for matched pairs than for unmatched pairs ($p < 0.001$) and for swapping pairs ($p < 0.05$), although the latter difference was not significant under the modified $\alpha$-value. Moreover, swapping pairs yielded a higher perceptual duration than the unmatched pairs ($p < 0.001$).

Discussion

The results show that the type of shape pairing affects perceptual durations, especially in the colliding surfaces condition, which indicates that identity ambiguity plays a role in the perception of symmetric surfaces. The effects are small, however, so that even interpretations that are not compatible with the stimulus manipulation can be readily perceived (in these cases, elements seem to change their shape when crossing the vertical midline). Possibly, these effects might be increased by increasing the difference between the elements, for instance by “labeling” elements with additional stimulus dimensions, such as size or color.

The pattern of effects is different for each kind of percept. In case of the rotating cylinder, unmatched pairing elicits the highest perceptual duration. This is according to the expectation because unmatched pairings give the most unique specification of a rotating cylinder. Disambiguation also has a positive effect on the colliding surfaces percept but not on the crossing surfaces percept.

For both types of symmetric surfaces percepts, the ambiguous matched pairs condition yielded longer perceptual durations than the non-ambiguous conditions. A possible explanation is that, in the matched pairs condition, fine-scale symmetry is preserved but it is violated in the other conditions. In other words, in the matched pairs condition, not only the positioning of elements is symmetric; the elements themselves are also symmetric with respect to each other. Together with the previous experiment, this suggests that the symmetric surfaces percepts are supported by symmetry processing at both fine and rough spatial scales simultaneously.

General discussion

Most research on multi-stable stimuli points at the competition between high-level perceptual interpretations rather than low-level stimulus features (e.g., Grunewald, Bradley, & Andersen, 2002; Kornmeier & Bach, 2005; Parker, Krug, & Cumming, 2002; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Similarly, in the SFM literature, it has been argued that the competition between different perceptual interpretations, for instance, clockwise versus counterclockwise rotating cylinders, is resolved at the level of surface perception (e.g., Brouwer & van Es, 2006; Hol et al., 2003; Klink et al., 2008; Treue et al., 1995, 1991). For instance, Brouwer and van Es (2006) showed that, if the surface of a rotating cylinder features a patch with a high dot density, perceived rotation direction tends toward the motion direction of the surface containing the patch. Crucially, the same effect is found if the patch contains no dots at all, although elements moving in the opposite direction are visible through the gap. This suggests that the dominance of a perceptual interpretation depends on the salience of the motion and not so much on the competition between individual elements.

In all of our experiments, perceptual durations for the different interpretations added up to more than 20 s (22–24 s in Experiments 1 and 2, and up to about 32 s in Experiment 3), which suggests that voluntary control is involved in surface perception. This implicates that perceptual competition takes place at a level of processing that can be targeted by voluntary control. We propose that this level is the level of surface perception, because the different interpretations of the symmetric motion stimulus differ mainly in the perceived spatial arrangement of surfaces. The importance of surfaces in visual perception was corroborated by Wannig et al. (2007), who showed that visual attention can target motion-defined surfaces and that, moreover, attention to surfaces modulates the activity of MT/V5 neurons. Given this evidence, it seems safe to conclude that the perceptual competition between the rotating cylinder percept and the symmetric surfaces percept is also resolved at the level of surface perception.

The present stimulus is truly multi-stable in the sense that there is not only competition between the rotating cylinder and symmetric surfaces, but there is also
competition between different rotating cylinders (clockwise or counterclockwise rotation, and concave or convex surfaces) and different symmetric surfaces (crossing or colliding surfaces, and cyclic or winding motion). In the next two sections, we will expand on the possible determinants of the different symmetric surfaces interpretations and on the implications of the results for the neural implementation of structure-from-motion.

**Perceptual competition between different symmetric surfaces percepts**

As outlined in the Introduction section and as illustrated in Figures 1 and 2, symmetric surfaces can be perceived in a number of different variations. Two sources of ambiguity seem to govern the competition between these different interpretations.

**Ambiguous depth order**

In patterns of sinusoidally moving dots, depth order is inherently ambiguous. In the rotating cylinder interpretation, the same physical stimulus may be perceived as rotating clockwise or counterclockwise. Surface convexity/concavity can be assigned to the front and back surfaces independently so that one can also perceive two frontoparallel convex or concave surfaces (Hol et al., 2003).

Symmetry partly resolves this ambiguity by establishing relative depth relationships. Symmetrical elements “like to be” in the same depth plane and symmetry detection is hampered if symmetric elements are forced on different depth planes via stereo information (Treder & van der Helm, 2007). Therefore, in a symmetric interpretation of the stimulus, symmetric elements are assigned equal depth values. Consequently, what is an ambiguity of rotation direction in the rotating cylinder percept translates to an ambiguity of surface motion direction. Surfaces can be perceived as moving forward (toward the observer), as moving backward (away from the observer), or as moving in cycles. Figure 9 illustrates the conflict between grouping by motion and grouping by symmetry.

**Ambiguous element identity**

In perfectly symmetric stimuli, elements of symmetry pairs occlude each other at the vertical midline. When the elements move apart again, there is ambiguity as to which element is which. As shown in Experiment 3, “labeling” alone does not resolve this ambiguity completely, but, as illustrated in Experiment 2, preventing these occlusions by using surface symmetry rather than element symmetry makes the colliding surfaces interpretation disappear.

While the exact type of the symmetric surfaces percept is specified by these ambiguities, the number of perceived surfaces is not. In the pilot experiment, we noticed that the number of perceived symmetric surfaces can differ from stimulus to stimulus. We conjecture that this is caused by inhomogeneities in dot density due to the random placement of dots. For the rotating cylinder, patches of high or low dot density have been shown to affect perceptual reversals of rotation direction (Brouwer & van Ee, 2006). For the symmetric surfaces, patches with a relatively high density of elements are perceptually segregated from other patches. That is, surface interpolation takes place between the elements within the patches but, unlike in the rotating cylinder, surface is not extrapolated beyond the patches, resulting in a number of detached moving surfaces. The importance of high intensity patches is illustrated in Movie 4, where a limited-lifetime dot pattern is shown. In contrast to the stimuli used in Experiment 2, the dots are not replotted within pre-specified high-density surfaces but rather randomly on the screen. The rotating cylinder can still be perceived with this stimulus, but the perception of symmetric surfaces collapses. Due to the unconstrained repositioning of symmetry pairs, high-density clusters of dots are only transient, counteracting a stable and continuous representation of symmetric surfaces.
The results presented in this study also constrain models about the neural implementation of SFM. Neurally, SFM is supported by a cortical network spanning areas from the ventral and dorsal stream, such as MT/V5, V3A, and LOC (Orban et al., 1999; Paradis et al., 2000; Raemaekers et al., 2009; Vanduffel et al., 2002). Interestingly, 2D symmetry has also been associated with high levels of activation in V3A and LOC (the designated region for feature integration), but there was no symmetry-specific activation in MT/V5, the presumed “engine” of surface interpolation (Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Tyler et al., 2005). If, however, symmetry signals are not processed in or feedbacked to MT/V5, this implies that the interpolation of the symmetric surfaces is not completed in MT/V5 but rather in a higher tier area such as LOC.

Conclusion

In this study, we demonstrated the emergence of novel interpretations of the rotating cylinder stimulus when the underlying dot pattern is 2D symmetric. The results of three studies suggest that the new percepts are due to an interaction between SFM processing and symmetry processing and, furthermore, that the competition between motion-based percepts (i.e., the rotating cylinder) and symmetry-based percepts (i.e., the symmetric surfaces) is resolved at the level of surface perception. This shows that structure-from-motion is a highly interactive process that incorporates not only motion cues but also form cues.

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