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# Components of motion perception revealed: two different after-effects from a single moving object

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#### Abstract

If motion that one has been looking at for some time suddenly stops, or if one shifts one's gaze to a static object, one will see motion in the opposite direction: the motion after-effect. If two transparent surfaces move with different speeds in different directions, then the direction of the motion after-effect will depend on the test pattern. For such transparent surfaces both the local motion and the global percept have two components. When looking at a normal moving object, there is only one perceived global motion. However, we know that locally there can be considerable ambiguity (the aperture problem). Does one adapt to all the local components, including those that one does not perceive, or only to the perceived global motion? We designed a stimulus that is perceived to be a fast rotating object, but also has a slow local radial component of motion. By selecting an appropriate test pattern we could either get a radial or a rotating motion after-effect. Thus we show that adaptation to motion must (also) occur at a stage at which local motions have not yet been integrated to give a unified percept.

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## 1. Introduction

Often our perception does not entirely correspond with the physical stimulation. For example, when looking at a rotating and tightly wound spiral we perceive illusory expansion or contraction rather than rotation. Why does our percept correspond with a radial motion while the spiral is only physically rotating? The answer has to do with how the visual system integrates local motion signals. If we look at the stimulus through a small aperture (see Fig. 1A) then several interpretations are possible because it is not clear which points on the spiral should be compared. The interpretation that involves the least (i.e. slowest) motion is that the curved line is moving radially, and this is what we perceive. The ambiguity within the small window is known as the aperture problem and it presumably arises at V1 where neurons have small receptive fields. Supposedly, our percept of the spiral's global motion arises when neurons with large receptive fields integrate the activity of local signals from earlier stages (Morrone, Burr, & Vaina, 1995). An area in which neurons are sensitive to global radial (as in the spiral) and rotational motion is MSTd (e.g. Tanaka & Saito, 1989).

If we look at a static test pattern after adapting to the moving spiral we experience a motion after-effect (MAE) that is in the opposite direction than the previously perceived illusory radial motion, rather than opposite the physical rotation. Although the radial MAE is in the opposite direction than the previously perceived motion, we cannot be certain that the adaptation takes place after the local motion signals

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Fig. 1. Images of a rotating spiral at two moments in time: (A) illustration of the local radial motion component of a physically rotating spiral. Local radial motion is present within the circular aperture (dashed circle) because points at time 1 (dashed spiral) are matched with the nearest points at time 2 (solid spiral) rather than with the same point on the spiral. This leads to the percept of slow radial motion (black arrow) rather than fast rotational motion (coloured arrows) and (B) our stimulus was part of a black spiral with a total radius of 6.8 cm. Locally both radial and rotational motion are present within the circular aperture (dashed circle).

have been combined to give a global percept, because local after-effects could also be combined to give this global percept. This is not a new idea. For instance, Verstraten, van der Smagt, Fredericksen, and van de Grind (1999) have pointed out that a perceived global MAE could be the result of integrating two local after-effects. They did so when discussing their original suggestion that the unidirectional perceived MAE after exposure to two transparent surfaces moving at the same speed in different directions is evidence that the MAE arises at a single locus of adaptation beyond the site of integration (Verstraten et al., 1999). Thus determining at what level adaptation takes place is not simple. Moreover, there is evidence that both local and global mechanisms contribute to the MAE (Culham, Verstraten, Ashida, & Cavanagh, 2000; Snowden & Milne, 1997; Verstraten et al., 1999). For instance, Snowden and Milne (1997) demonstrated an MAE in parts of the visual field that were not stimulated at all. The MAE was in the opposite direction than the perceived, global interpretation of the adapting stimulus, but it was weaker than the MAE at the stimulated locations. In studies such as that of Snowden and Milne, the global percept during adaptation is consistent with the local motion within the stimulated parts of the scene. In the present study we examine what happens when local motion signals are inconsistent with the global percept.

After adapting to two transparent surfaces moving at different speeds (slow and fast), the direction of the MAE depends on the type of test pattern (van de Grind, van Hof, van der Smagt, & Verstraten, 2001; van der Smagt, Verstraten, & van de Grind, 1999; Verstraten et al., 1999). If a static test is used we perceive an MAE opposite the slow component; if we use a dynamic test (e.g. like a detuned TV) then the MAE is opposite the fast component. This finding suggests that there are two motion channels, which adapt independently at the same level of visual processing (e.g. Verstraten et al., 1999). Dynamic test patterns can also reveal after-effects of non-luminance based motion (e.g. Nishida & Sato, 1995), but we are only concerned with luminance-based motion in the present study. We here use the fact that the after-effect that one measures depends on whether the fast or the slow motion channel is activated by the test pattern to design a stimulus for which we predict a different MAE on the basis of the local motion signals than on the basis of the global percept.

Since transparent motion involves segregation at a global (perceptual) level, it cannot be used for separating local from global contributions to the perceived MAE. In order to introduce an inconsistency between the global percept and local motion signals we used a fragment of a spiral with several additional conspicuous shapes (see Fig. 1B). When this pattern rotates, one sees a global rotation, without any conspicuous expansion or contraction. This is not surprising, because adding squares and circles and removing half of the spiral make it clear that the global motion of the stimulus is a rotation. This fast rotation masks the slow radial motion component that is still present locally in half of the pattern (see circular window in Fig. 1B). Therefore, if adaptation (predominantly) occurs after the integration stage, we expect to see a rotational MAE, because that is the type of motion that is perceived. However when subsequently exposed to a static test pattern, 13 subjects all saw a radial MAE (see Section 3). Thus the subjects have an after-effect of a component of motion that they did not see.

Following the above reasoning, this result shows that adaptation does occurs at a stage before that at which the different components are integrated to form a coherent percept. If this interpretation is correct, then subjects should not only have adapted to the unperceived slow radial component, but also to the fast rotational component. To investigate whether this also happened we made use of the test pattern dependency of the MAE that we already mentioned in relation to the different channels for slow and fast speeds. We assume that this dependency is not special for transparent motion, but also holds for the components of our coherently moving stimulus. If so, the rotational and radial components, which move, respectively, at fast and slow speeds, should selectively stimulate the fast and slow motion channels (Edwards, Badcock, & Smith, 1998; Gegenfurtner & Hawken, 1996; van de Grind, Koenderink, & van Doorn, 1986) to elicit two different directions of MAE, depending on the test pattern. We expect that subjects do not only see a radial MAE for a static test pattern (as mentioned above), but also a rotational MAE if the test pattern is dynamic. The results confirmed this.

## 2. Methods

## 2.1. Participants

Thirteen participants, including the authors, took part in the experiment. Everyone had normal (corrected) vision.

## 2.2. Adapting stimuli

The spiral consisted of 158 line-segments with a new segment every 14 degrees (either in clockwise or anticlockwise direction in the image plane), and a radial increment of 0.0432 cm per segment (see Fig. 1B). Half of the spiral was removed to reduce the clarity of the local radial component. Black squares and circles were added to ensure that subjects saw the fast rotational motion. The half-spiral and additional black figures were presented on a white background at a viewing distance of 90 cm. The animation was shown at 85 Hz using a resolution of 40 pixels/cm.

To test the above-mentioned prediction, we tuned the speeds of the rotational and radial components of our fragmented spiral so that the rotation would mainly activate the fast channel while the radial motion would mainly activate the slow channel. The stimulus rotated at 1.9 Hz, giving an angular speed that increased linearly with eccentricity (up to 45 deg/s) and a local radial component (2.08 cm/s=1.16 deg/s) that was independent of eccentricity. A clockwise spiral moving in a clockwise direction gives rise to local expansion, as does an anti-clockwise spiral moving in an anti-clockwise direction.

The other two combinations give rise to local contraction. We refer to the four combinations of two spiral directions and two directions of rotation as: clockwiseexpansion, clockwise-contraction, counter-clockwiseexpansion and counter-clockwise-contraction. One can view a demo of the stimulus at http://www.ub.es/pbasic/visualperception/joan/en/demos.html.

# 2.3. Procedure

On each trial we presented one of the four motion combinations for 12 s, followed either by a static or a dynamic test pattern. The test pattern consisted of 300 randomly placed dots within a circular (6.84 cm diameter) window placed at the centre of the spiral. The dots were presented for two seconds, and were either static or refreshed every 12 ms (dynamic). The eight combinations of adapting stimulus (n=4) and test pattern (n=2) were each presented ten times in a random order (giving a total of 80 trials). Subjects were asked to indicate after each trial whether the test pattern was expanding, contracting, rotating in a clockwise or rotating in a counter-clockwise direction (four alternative forced choice). To test whether individual subjects could detect the radial component, they were asked to indicate after 10 s of adaptation (marked by a short green flash) whether the half-spiral was expanding or contracting. They had to respond by pressing one of two keys within the 2 s before the test pattern appeared. If they failed to do so a tone sounded and the trial was repeated.

## 3. Results

Fig. 2 shows that our hypothesis is confirmed: the static test pattern mainly elicited radial responses in the opposite direction than the local radial motion in the adaptation phase (expansion or contraction; 89%), whereas the dynamic test pattern mainly elicited rotational responses in the opposite direction than the rotation in the adaptation phase (85%). On questioning after the experiment, none of the subjects reported simultaneously seeing rotation and radial motion in any of the conditions.

Due to the fragmentation, the radial component of motion is not only no longer dominant, but it is even difficult to detect. As can be seen in Fig. 3, some subjects failed to perform above chance when they were asked to indicate the radial direction of the stimulus. Even those that performed well found this quite a demanding task. In contrast, for the static test pattern all subjects reported a compelling after-effect in the opposite direction to that of the radial component in the adaptation phase.



Fig. 2. Proportion of each of the four possible responses as a function of the combination of adapting motion and test pattern. The responses are generally in the opposite direction than one of the local motion components of the stimulation (thick red pattern). The static test pattern yields mainly radial after-effects (dotted), whereas the dynamic test pattern yields mainly rotational after-effects (striped).



Fig. 3. Relation between the detection of radial motion and the MAE that it induces in a static test pattern. Each symbol represents one subject. The grey region denotes the 95% confidence interval for chance performance in detection. The chance level for the MAE responses is 25% (not shown). Although several subjects could not reliably detect the radial component of the adapting stimulus, all subjects had a very clear after-effect in the opposite direction than this component.

## 4. Conclusions

Previous studies have shown that the MAE is a very complex phenomenon that depends on many factors. In the present study we only consider two stages of visual processing: the local motion signals and the global percept. Our results show that when the conditions are such that adaptation at these two stages is expected to result in different after-effects, the MAE is most consistent with adaptation at the local motion signal stage. The global MAE presumably arises by combining these local after-effects. Selectivity of the (rotational) MAE to factors such as the eye that is stimulated and whether stimulation is monocular or binocular (Anstis & Duncan, 1983) suggests that this local adaptation takes place quite early in the visual system (presumably in V1). This conclusion is consistent with previous studies (e.g. Wade, Spillmann, & Swanston, 1996) that describe the MAE as the global expression of adapting local regions to motion. These findings not only show that adaptation to motion is primarily a local process, but they also show that these local processes are not disrupted by the process of combining local possible interpretations into a single coherent motion percept (i.e. solving the aperture problem). This could not be concluded from studies using transparent motion, because in such studies the different local components were not combined; they remained visible as segregated global linear motions. The finding that the unperceived component of motion does give rise to an MAE means that the neurons that are normally responsible for this component are active during the adaptation phase. Thus our findings imply that the process of reaching a single coherent percept does not involve suppressing local activity by feedback from "higher" motion areas (Lamme & Roelfsema, 2000). Instead, the coherent percept presumably arises from spatial interactions between the inputs from many speed (or frequency) tuned neurons. Such interactions, at stages that we have not considered in the present paper, must also be responsible for the after-effects in regions that were never stimulated (Snowden & Milne, 1997).

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