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Motion distorts perceived position without awareness of motion

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A number of striking illusions show that visual motion influences perceived position [1]; in all of these, the perceived shift is accompanied or preceded by a visible and salient motion signal. Observers can easily scrutinize the motion: they can attentively track, or at least perceive via inference, the moving features [2–4]. With position shifts that accompany the motion aftereffect (MAE) [5–10], for example, observers can attentively track the moving adaptation stimulus [11,12]. Even if the shifted test pattern does not display any perceived motion [6,10], the moving adaptation stimulus is clearly visible, and it could be the visibility of the adaptation stimulus that causes the perceived shift in the test stimulus position. If awareness of motion, mediated by high-level or top-down mechanisms, explains all motion-induced position shifts, then there should be no shift in perceived position without the perception of directional motion. Here, we show that perceived position can be shifted even without awareness of motion.

To test whether the awareness of motion is necessary to shift perceived position, we used a crowding technique developed by He and colleagues [13]. Figure 1 shows the basic stimulus: an array of drifting Gabor patterns (moving sine wave gratings with static gaussian envelopes). The number and spacing was such that subjects were not aware of, or able to report, the direction of motion in any of the central Gabors (see Supplemental data available with this article online). Each Gabor contained either leftward or rightward motion, determined randomly on each trial. Two vertically aligned pairs of

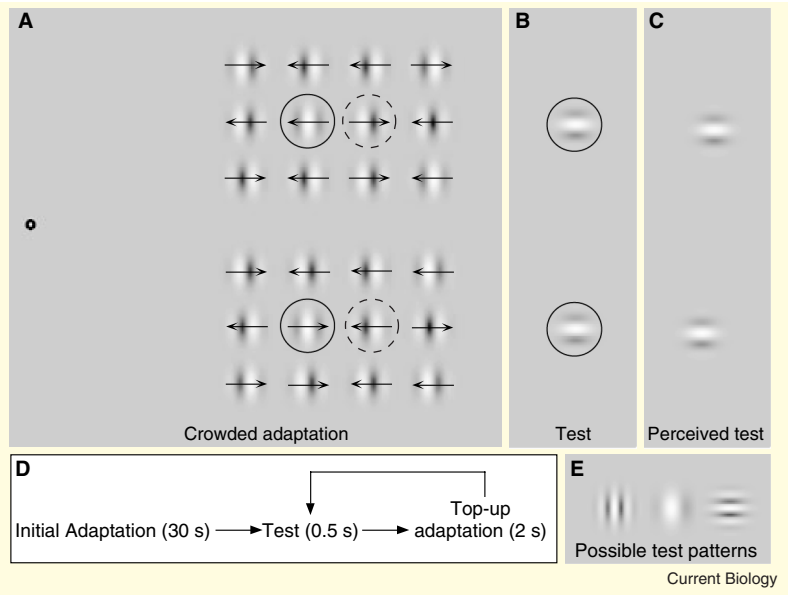

Figure 1. Stimuli used in the first experiment.
(A) An array of Gabor patches was presented for an adaptation period while subjects fixated on the bull's-eye. Two pairs of vertically aligned Gabors in the central region of the array had opposing directions of motion, which was fixed throughout an experimental session (adapted regions are circled by dashed and solid lines, respectively; these circles are for illustration and were not presented in the actual stimulus). All other Gabors served as crowding stimuli and had randomly determined directions of motion (leftward or rightward) on each trial. (B) During the test period, two static Gabors were presented in one of the two vertically aligned, adapted regions. (C). After adapting to the stimulus in (A), the test Gabors in (B) appear to be misaligned in a direction opposite that of the prior motion adaptation. (D) Each session began with an initial adaptation period, followed by a repeat test and top-up adaptation periods. (E) Examples of several different kinds of test Gabors that could be presented during the test period.

Gabors, however, had motion that was always in opposite directions (dashed and solid circled regions in Figure 1A), providing a consistent adaptation direction across trials. After each trial, the array of Gabors was removed, and a single pair of static test Gabors was presented (Figure 1B), located in either of the regions that were previously adapted to motion (either the solid or dashed circled region in Figure 1A).

Because of the crowding, subjects were unable to identify the direction of motion presented within any of the adapted regions (correct direction judgments were not significantly different from chance in the crowded region, provided this was greater than ~20 deg from fixation; see Figure S2 in Supplemental data). Although subjects were unaware of the direction of motion during adaptation, there was a significant shift in the perceived position of the test stimuli (Figure 2).

The perceived shift in the position of the test Gabors was always in a direction opposite that of the motion adaptation and could be mediated by awareness of motion during the test period. To rule out the possibility that subjects attended to a passively generated motion aftereffect during the test period, we presented orthogonally oriented test Gabors. McGraw and colleagues [6] have shown that this manipulation effectively eliminates the perceived MAE in the test stimuli, but leaves intact the perceived position shift. Figure 2B (solid symbols) shows that there was still a perceived shift in the positions of the test Gabors, even with their orthogonal orientation ($t_{(3)} = 4.25$, $P < 0.02$). The local nature of the motion adaptation, and the randomized directions of motion in the array of Gabors, suggest that an ensemble pattern [14] did not contribute to the results.

If subjects became aware of the direction of motion in the adaptation Gabors, this could have influenced judgments on subsequent trials. Two additional

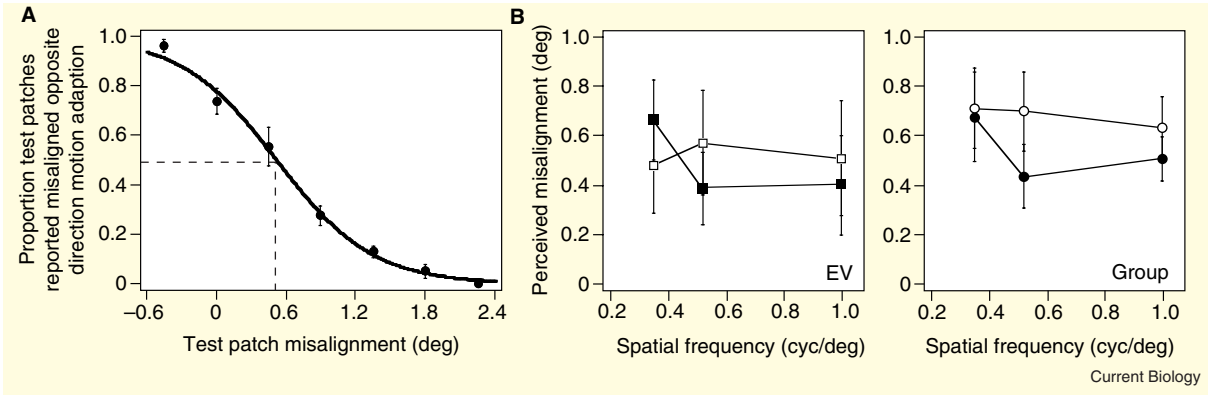

Figure 2. Results of the first experiment.
(A) A representative psychometric function showing a significant shift in the perceived position of the test Gabors as a function of the direction of motion adaptation. The abscissa shows the physical misalignment between the test Gabors: positive values indicate that the Gabors were misaligned in the same direction as the prior motion adaptation, and negative values indicate that they were misaligned in a direction opposite that of the motion adaptation. The ordinate shows the proportion of trials in which the subject perceived the test Gabors to be misaligned opposite the direction of the prior motion adaptation. The point of subjective equality (PSE, the inflexion point) defines the physical misalignment between the Gabors that appeared to be aligned. Because of the motion adaptation, the Gabors had to be presented ~0.6 deg in the same direction as the prior motion adaptation to appear aligned ($t_{(7)}$ = 6.06, P = 0.001). When physically aligned, the Gabors appeared shifted opposite the direction of the motion adaptation. (B) Results for one representative subject (left panel), as well as all four subjects averaged (right panel), as a function of the spatial frequency (abscissa) and orientation of the test Gabors. The orientation of the test Gabors was either the same as (open symbols) or orthogonal to (solid symbols) the orientation of the adaptation Gabors. There was a significant shift in the perceived position of the Gabors with both test orientations (same orientation: $t_{(3)}$ = 4.8, P < 0.01; orthogonal orientation: $t_{(3)}$ = 4.25, P < 0.02). Across all subjects, there was little variation in the illusory position shift as a function of spatial frequency ($F_{(2,6)}$ = 2.6, P = 0.15). There was a larger perceived shift when the test stimuli contained the same orientation as the adaptation stimuli, although this difference did not reach significance (for the group results in the right panel, $t_{(3)}$ = 2.75, P = 0.07). There was a significant overall position shift for each individual subject as well (least significant effect was for subject EV, $t_{(5)}$ = 5.96, P = 0.002; the least significant within-subject condition effect for subject EV was the orthogonally oriented test Gabor with a spatial frequency of 1 cyc/deg: $t_{(30)}$ = 3.3, P < 0.01). Error bars ± s.e.m.

experiments were conducted to address this potential problem. In one, each pair of adaptation Gabors contained a randomly determined direction of motion on each trial (leftward or rightward, in contrast to the first experiment where the direction of motion in the adaptation Gabors was fixed across trials). So, the motion adaptation was only guaranteed to accumulate over a single 8 second trial. Although less than ideal for generating directional motion adaptation, this ensures that even if subjects become aware of the direction of motion adaptation on one trial, this knowledge or awareness is not informative and cannot bias judgments on subsequent trials. To avoid the saturation that occurs when both directions of motion are sequentially adapted, the fixation point was repositioned on each trial, ensuring that adaptation occurred at different retinal locations (see Supplemental data). Despite the brevity of the motion adaptation, there was still a significant shift in the perceived positions of the test Gabors (Figure S1 in the Supplemental data), and subjects were unable to identify the direction of motion in the adaptation Gabors (Figure S2).

A third experiment differed from the second only in that each of the crowding Gabors in the array had a randomly determined orientation spanning the entire 360 deg range. This eliminates (or at least dramatically reduces) the possibility that on any particular trial there might be a net difference in the direction of motion presented in the adaptation and crowding Gabors (which could serve as a perceptual grouping cue that might break crowding). Local motion adaptation still produced a significant shift in the perceived positions of the test Gabors (Figure S1).

The results here show that adaptation to motion, even without awareness of the adaptation or any motion aftereffect, can shift the perceived positions of stationary objects. Therefore, perceived position shifts do not entirely depend on high-level (top-down) mechanisms responsible for attentionally driven or inferred motion. Low-level motion does contribute to perceived position, consistent with mounting physiological evidence that the coded location of an object can be influenced by motion at very early stages of visual processing — even as early as the retina [15] and primary visual cortex [16,17]. These low-level mechanisms do not preclude high-level processes, such as attentive tracking; indeed, the experiments reported here support the idea that there are both types of mechanism: a passive, bottom-up motion detector that influences coded location as well as another mechanism mediated by high-level processes associated with awareness of motion.

Supplemental data

Supplemental data containing additional references and experimental procedures are available at http://www.current-biology.com/cgi/content/full/15/9/R324/DC1/

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The *Schizosaccharomyces pombe* imprint — nick or ribonucleotide(s)?

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The nature of the *Schizosaccharomyces pombe mat1* imprint, which acts to initiate mating-type switching, has been a subject of dispute. The imprint was proposed to be a site- and strand-specific nick [1]. Meanwhile, our work has shown i) that imprinted DNA can be purified such that both *mat1* strands are intact, ii) that imprinted *mat1* DNA can be broken by alkali or RNase treatment, and iii) that two populations of imprints exist, where either one or two ribonucleotides have been incorporated into the *mat1* DNA, creating a DNA–RNA–DNA hybrid strand [2,3]. A recent paper by A. Kaykov and B. Arcangioli presents data that the authors claim 'are in disagreement with the RNA model and strongly indicate that the imprint is a nick' [4]. However, our analysis suggests that Kaykov and Arcangioli's data are fully compatible with the imprint being RNA in nature.

It has long been known that the *S. pombe mat1* imprint is labile during purification. Are the data presented by Kaykov and Arcangioli consistent with a nick being formed during purification due to hydrolysis of a ribonucleotide imprint? In the presented paper, it is assumed that the hydrolysis of an RNA imprint always leaves a gap [4]. However, when a DNA–RNA–DNA hybrid molecule, consisting of only one ribonucleotide incorporated into a DNA strand, is hydrolysed at the ribose residue, the ribonucleotide will stay attached to the 3′ end of the 5′ fragment and a nick will be present. Only if the hybrid molecule contains two or more consecutive ribonucleotides will a gap be formed by the hydrolysis (see below).

Kaykov and Arcangioli detect the nick in *mat1* DNA using different enzymatic activities and assays, but do not address whether their results are compatible with the RNA nature of the imprint. The enzymes used in their study (*Escherichia coli* DNA ligase, *Pst*I restriction endonuclease and Taq DNA polymerase) are assumed to act specifically on DNA. However, the activities of these enzymes on substrates resembling either an intact or hydrolysed ribonucleotide imprint are not tested. Our unpublished characterization of these enzymes shows that they are able to utilize such substrates. In particular, Taq DNA polymerase can efficiently elongate across up to three ribonucleotides; *E. coli* ligase can ligate a nick in a duplex substrate where a single ribonucleotide provides the 3′ hydroxyl group that is to be ligated to the 5′ phosphate; and *Pst*I can restrict a recognition site containing a single ribonucleotide. Thus, none of these enzymatic activities can be used to discriminate between the two models, and the presented data are therefore equally consistent with the imprint being ribonucleotide(s) as with it being a nick.

Our previously published work suggested that the imprint could be either one or two ribonucleotides; therefore, in the wild-type situation hydrolysis of the imprint will lead to the formation of either a nick or a one-nucleotide gap. Importantly, none of the experiments aimed at addressing this issue contradicts our results or model. Firstly, in a set of presented LM-PCR experiments, an adaptor is ligated to the 5′ end of the nick observed at *mat1*. The adaptor was designed such that it can be ligated only to molecules where there is a nick present at the *mat1* imprint, as missing nucleotide(s) will create a gap inhibiting ligation. In the subsequent LM-PCR, efficient amplification is observed, and it is concluded that the imprint is a