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# Strong perceptual consequences of low-level visual predictions: A new illusion

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ABSTRACT

Predicting information is considered to be an efficient strategy to minimise processing costs by exploiting regularities in the environment, and to allow for adaptation in case of irregularities, i.e. prediction errors. How such errors impact conscious perception is unclear, especially when predictions concern elementary visual features. Here we present results from a novel experimental approach allowing us to investigate the perceptual consequences of violated low-level predictions about moving objects. Observers were presented with two squares moving towards each other with a constant speed, and reported whether they were in contact or not before they disappeared. A compelling illusion of a gap between the squares occurred when the leading edges of those squares contacted briefly. The apparent gap was larger than a physical and stable separation of 2.6 min of arc between the squares. The illusion disappeared only when the contact did not violate extrapolations of the contrast edge between the moving object and the background. The pattern of results is consistent with an early locus of the effect and cannot be explained by decisional biases, guesses, top-down, attentional or masking effects. We suggest that violations of the contrast edge extrapolation in the direction of motion have strong perceptual consequences.

## 1. Introduction

We present here a new illusion, observed while looking for a way to explore the perceptual consequences of predictions and prediction errors. Two squares are moving towards each other, and disappearing from the screen immediately after the collision. We expected that the perception of collision would be facilitated by motion-related prediction mechanisms. However, contrary to our expectation, we saw a gap between the squares at the time of the collision. In the work reported here we tried to unravel the mechanisms underlying this illusion, and describe how we came to suggest that the key factor affecting the perceived gap is the change in contrast polarity between the leading edge of the moving object and the background when the squares collide.

It has been proposed that the visual system uses available information and regularities to predict the incoming sensory input. A great body of experimental evidence supports the hypothesis that information about the incoming sensory input is being predicted across the visual hierarchy (Berry, Brivanlou, Jordan, & Meister, 1999; Duhamel, Colby, & Goldberg, 1992; Ekman, Kok, & de Lange, 2017; Hogendoorn, Carlson, & Verstraten, 2008; Roach, McGraw, & Johnston, 2011). As early as in the retina, object motion elicits a moving wave of activity of retinal ganglion cells (Berry et al., 1999). Similar evidence has been found in the early visual cortex where features of the signal are processed (e.g. Benvenuti et al., 2020; Fu, Shen, & Dan, 2001; Jancke et al., 1999), as well as later in the visual processing pipeline where the forms are identified and their relations interpreted (Leptourgos, Bouttier, Jardri, & Denève, 2020).

An influential hypothesis about how predictions are propagated across the hierarchy is predictive coding (Rao & Ballard, 1999). In the general predictive coding framework, regions at different stages in the processing hierarchy code both predictions and the mismatch between the predictions and incoming sensory information (prediction error; Friston, 2005; Kok & de Lange, 2015; Rao & Ballard, 1999). In addition, predictions and errors are communicated across the hierarchy, and it is

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necessary for the system to make them coherent (Leptourgos et al., 2020; Pins & Ffytche, 2003; Todorovic & de Lange, 2012). This strategy is considered to be efficient, since once a high-level representation is established, only error signals are propagated through the visual system, minimising energy spent in processing predictable or unchanging input (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Kerzel & Gegenfurtner, 2003; Schellekens, van Wezel, Petridou, Ramsey, & Raemaekers, 2016).

In general agreement with the predictive coding hypothesis, it has been suggested that higher-level expectations can modulate activity in early sensory areas (Kok, Failing, & de Lange, 2014; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Todorovic & de Lange, 2012). These prior expectations can activate primary sensory cortex in the absence of expected information (Kok et al., 2014; Muckli et al., 2005) or attenuate processing of incoming sensory information (e.g. Todorovic & de Lange, 2012; Van Humbeeck, Putzeys, & Wagemans, 2016). Furthermore, predictions of incoming sensory information can be decoded from the brain activity ahead of the actual sensory input, and a response to novelty is elicited in the case of prediction violations (Blom, Feuerriegel, Johnson, Bode, & Hogendoorn, 2020; Wacongne et al., 2011). These prediction errors do not necessarily change our perception but rather help us to attract attention or adapt to the error. As stated above, our approach is based on moving forms, as is also the case in many studies related to predictive coding. Several studies reported motion-induced shifts of neural activity in the direction of motion in visual cortex, in conditions where perceptual shifts were not observed (Maus, Fischer, & Whitney, 2013; Sundberg, Fallah, & Reynolds, 2006). Similarly, when a stimulus moves in regular steps across the screen, its location ahead of the physical stimulation can be decoded in the EEG activity, even when the subsequent stimulus is omitted (Blom et al., 2020). It is an open question whether in case of an omission, an illusory stimulus is seen at its implied future position. More generally, the question is whether predictions errors (and not predictions per se, Aru, Tulver, & Bachmann, 2018), lead to specific perceptual, subjective experience.

Perceptual consequences of prediction mechanisms have already been proposed. Several perceptual effects such as the flash-lag (a briefly flashed stimulus is seen to lag behind a continuously moving stimulus in its spatial proximity; MacKay, 1958) or representational momentum (seeing the final position of a moving stimulus ahead of its physical position, e.g. Freyd & Finke, 1984; Hubbard, 2005) are often interpreted as a consequence of a motion extrapolation mechanism: the perceived position of a moving object is affected by inherent predictions of its position in the direction of motion (for a review see Hogendoorn, 2020 and Hubbard, 2019, although Brenner & Smeets, 2000). Nevertheless, it is not clear at what level in the hierarchy these predictions are made, and whether they are accomplished by low-level sensory mechanisms (e.g. Fu et al., 2001), or are the consequences of cognitive interpretations. Yet, there are some reports suggesting low-level, sensory predictions are implicated in the perception of visual motion (Roach et al., 2011; Van Humbeeck et al., 2016). For example, it has been shown that the local prediction of a moving grating at the leading edge selectively improves the detection of a low contrast stimulus (Roach et al., 2011). The improvement was restricted to stimuli that share the phase and orientation of the grating. The importance of this work is that it showed that the sensory, i.e. low-level predictions, can have very specific perceptual consequences, since they specify the characteristics of the incoming pattern, rather than simply increasing gain or modulating attention (Roach et al., 2011; Van Humbeeck et al., 2016). However, there were no consequences of erroneous predictions on the detectability of stimuli. In fact, sensory processing has been found to be attenuated when the prediction is correct, not when it is erroneous (Blakemore, Wolpert, & Frith, 1998; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Martikainen, Kaneko, & Hari, 2005). We might still lack the proper tools and experimental protocols to assess the perceptual consequences of erroneous predictions.

In the work reported here, we present results from a novel experimental approach that allows us to investigate the perceptual consequences of violated low-level predictions about moving objects. Observers were presented with two squares moving towards each other with a constant speed. Once the stimuli stopped, they remained in contact for a variable duration, and observers reported whether they perceived them to have contacted or not before disappearing. As already emphasized, a great body of work suggests extrapolation of an object's position in the direction of its motion, predicting a strong percept of contact between the two squares (e.g. Hogendoorn, 2020). This prediction is also consistent with an intuitive expectation that two objects moving towards each other will make contact. We did not find evidence for facilitation of the perception of contact during our experiments. In contrast, we found that for short contact durations (< 33 ms), the perception was that stimuli had not contacted each other. In a series of experiments, we showed that the effect is not due to the inability to process briefly presented sensory information, transient offset masking, or a local gain control mechanism, but it is strongly dependent on contrast polarity of the stimuli, suggesting that the violation of extrapolations of the luminance edge between the moving object and the background have strong perceptual consequences.

## 2. General methods

### 2.1. Stimuli and apparatus

Stimuli were squares, size 0.9 × 0.9 (Experiment 1) or 0.7 × 0.7 degrees of visual angle (Experiments 2–4). In Experiment 1, the squares were grey, presented on the white background. In Experiments 2 and 4, the squares were black, and the background was mid-grey. In Experiment 3, the background was mid-grey, and the luminance of the squares varied in four steps across trials.

In Experiment 1, stimuli were presented on a Dell CRT screen, resolution 1280 × 1208 pixels and 60 Hz. The experiment was run in Matlab 2008. In Experiments 2–4, stimuli were presented on a Trinitron Sony CRT, resolution 1280 × 1208, and Matlab 2011 was used for programming and displaying stimuli.

### 2.2. Observers

In total, 56 observers participated across the four experiments: 16 in Experiment 1 (average age 28.1 years, 9 women); 12 in Experiment 2 (average age 26 years, 10 women) and Experiment 3 (average age 23.2 years, 9 women); and 16 in Experiment 4 (average age 28.3 years, 12 women). Sample sizes were determined based on previous studies of visual perception and psychophysics with repeated designs which conventionally use similar or smaller sample sizes (e.g. 8 in Maus & Nijhawan, 2006; 11 in Roach et al., 2011). No a priori power analysis was performed.

### 2.3. Data analysis

We analysed data with generalised linear mixed-effect models, implemented in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) for R Studio environment. This method of analysis has the ability to model between subjects variability and treat unbalanced designs (Bates et al., 2015). Here we describe a general structure of the models, and details concerning specific experiments are given in the results section of the experiment. Responses of observers were the dependent variable (binary responses), and predictors were the duration of the contact and square layout (filled or contour-only, Experiment 1) and speed of stimulus movement (Experiment 4). In Experiment 3 there were several analyses, described in detail in the results section. Observers were treated as a random factor, to account for the additional variability. To test models, we used ANOVA function implemented in R, which tests the significance of a fixed effect, by comparing the goodness-of-fit between the full model (including that fixed effect) and the model that does not include that variable as the fixed effect, by means of a Chi-square test. In order to obtain an estimate of how well the model explains the data, we used marginal $R^2$ as outlined in Nakagawa and Schielzeth (2013). In Experiment 2, we used the quickpsy package for R to fit psychometric functions to the data (Linares & López-Moliner, 2016).

## 3. Experiment 1: the violation of local luminance edge extrapolation has perceptual consequences

Experiment 1 was designed to test our observation of a gap between squares once they had contacted and disappeared from the screen. We also aimed to test whether our choice of stimuli layout and their transient disappearance affected the perceived spatial position of a single stimulus, with an experimental protocol similar to the one used to test the representational momentum.

### 3.1. Procedure Experiment 1A

We presented observers with two grey squares on a white background, moving towards each other with a constant velocity. Each trial started with a fixation point presented at the centre of a white screen (90 cd/m$^2$). Then, the fixation point disappeared and two grey squares (29 cd/m$^2$) appeared at either side of the fixation point, at an

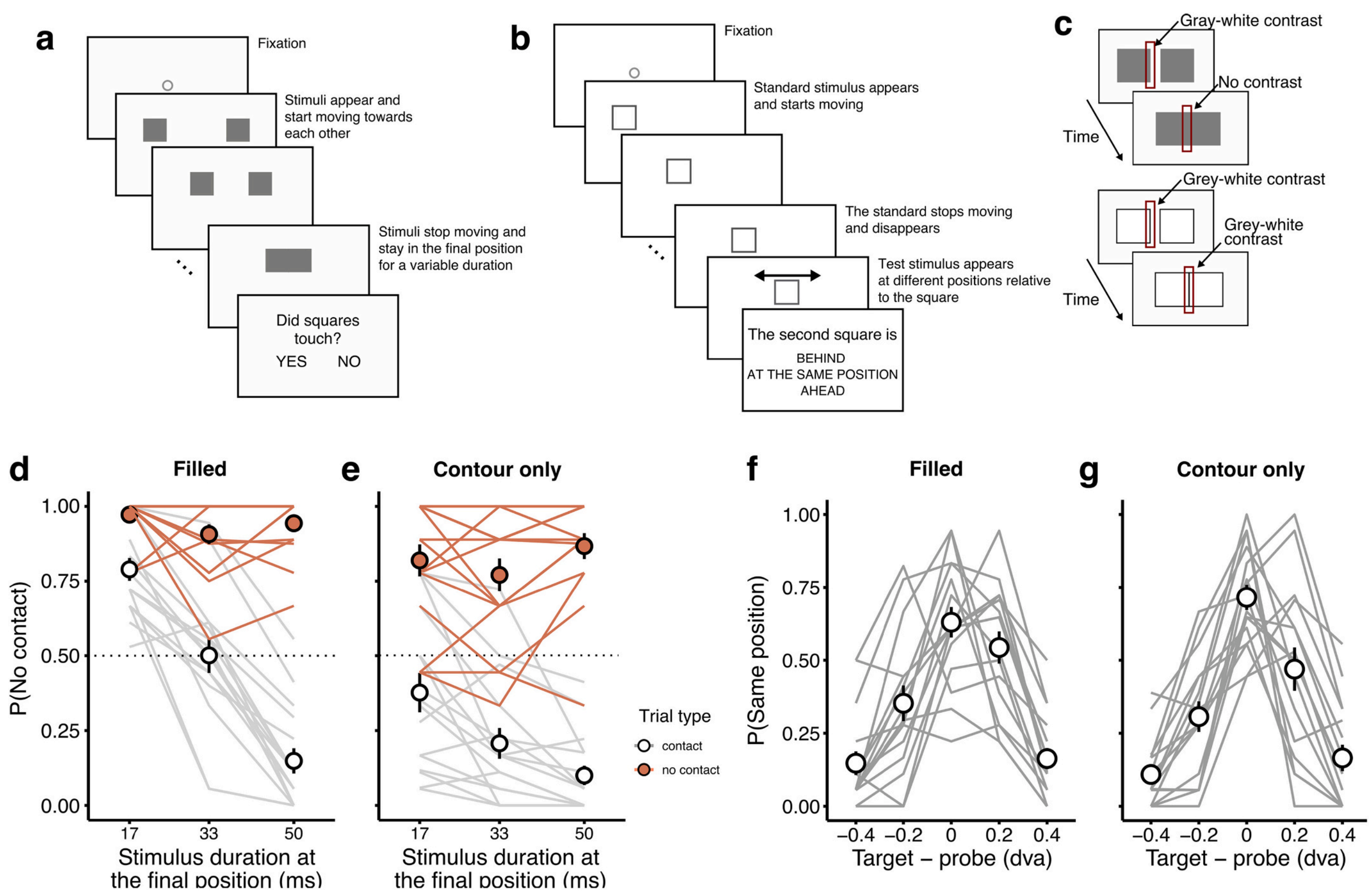


**Fig. 1.** Procedure and results of Experiment 1A and B.
(a) Schematic representation of the stimuli sequence in Experiment 1A. Each trial started with a fixation point. Then two squares appeared at different sides of the fixation point and started moving towards each other with a constant velocity. The squares stopped moving either when their edges came in contact, or before contact. After a variable duration, the squares disappeared and participants reported whether they perceived them to be in contact at the end of the trajectory or not. The panel shows the condition in which grey squares (filled) were presented.
(b) Schematic representation of the stimuli sequence in Experiment 1B. Each trial started with a fixation point. Then a standard stimulus appeared to the left or to the right of the fixation point, and started moving across the screen with a constant velocity. After the standard stopped and disappeared, a test stimulus appeared on the screen. Participants reported whether they perceived the test to be behind, at the same position or ahead relative to the motion direction of the standard square. The panel shows an example of the contour-only condition.
(c) Illustration of the rationale for including both filled and contour-only squares. In a condition in which the squares are grey and there is a physical separation between the two squares, there is a contrast difference at the leading edge and the background (here shown as grey-white contrast). When the squares contact, there is no difference in contrast at the leading edges. In a condition in which the squares are represented only with their contours, there is always a difference between the luminance at the leading edge (here shown as grey-white contrast).
(d-e) Results of Experiment 1A. The proportion of "no contact" (i.e. gap between the squares at their final position) responses is plotted against stimulus duration at the final location, separately for trials in which there was contact (grey lines and open circles) and trials with no physical contact between the squares (orange symbols). Performance in the two stimuli layout conditions (grey squares and contour-only) is shown in separate panels. For brief contact durations, participants reported an apparent gap between the two squares, which decreased with an increase in the contact duration. The effect was stronger in conditions in which grey squares (filled, panel d) were presented. On trials with physical contact between the squares, participants correctly detected the gap. Lines show individual performance, and circles indicate the mean across participants. Error bars indicate the standard error of the mean between participants.
(f-g) Results of Experiment 1B. The proportion of responses that the test stimulus was at the same position as the standard is plotted against the position of the test relative to the final position of the stimulus, separately for grey (panel f) and contour-only stimuli (panel g). Lines show individual performance, and circles indicate the mean across participants. Error bars indicate the standard error of the mean between participants.

eccentricity of 1.75 dva. The squares moved horizontally with a constant speed (1.4 dva/s). After stopping, they remained on the screen for 17, 33 or 50 ms. Once the squares disappeared, observers responded whether the squares were in contact or not ("Did the two squares touch"). On 30% of the trials there was no physical contact, at their final position the squares were separated by 2.6 arc min. We used a low percentage of trials with no physical contact, to avoid a high proportion of trials without detectable contact. We tested performance with two stimuli layouts: (1) the two grey filled squares or (2) squares represented only by their contours (contour-only condition), as illustrated in Fig. 1a and b. The contour-only condition was included to test whether there is an effect of the contrast difference between the leading edge of the moving object and the background before and after the contact. The grey level of the contours used in this condition was identical to the grey level used in filled squares, but, as shown in Fig. 1c, there was a contrast change at the leading edges only when the two grey squares contact. In that case the contrast at the leading edge of the moving object and the background changed from grey-white to grey-grey. In contrast, in the contour-only condition, the contrast at the leading edge remained grey-white (although the squares stopped when they were contiguous, and the width of the leading edge was doubled). The contact was always in the centre of the screen, but the vertical position of the squares varied between −2.2, 0 and + 2.2 deg., to match the variations used in Experiment 1B. The two conditions (filled squares and contour-only) were tested in separate blocks, with 81 trials in each condition. Each duration of contact was tested 18 times, and there were 27 trials with no contact between squares.

### 3.2. Procedure Experiment 1B

To test whether there is a perceived displacement of a single object's position at the end of its trajectory, we presented a standard grey square (29 cd/m$^2$, filled or contour-only) at eccentricity of 1.75 dva left or right from the fixation point, that began moving horizontally with a constant speed (1.4 dva/s) on a white background (90 cd/m$^2$), as in Experiment 1A. The standard square disappeared after stopping, and a test square was presented at one of five possible locations. The test was either presented at the same position as the standard, or displaced backward (−0.4 or − 0.2 dva) or forward (0.2 or 0.4 dva) relative to the standard's final position and direction of movement. The position of the squares was systematically varied in the 9 trials of a given condition, with both their vertical and horizontal position being displaced by −2.2, 0 or + 2.2 deg. Observers' task was to choose one of the three possible answers: the test is behind, at the same position, or ahead the final position of the standard relative direction of its movement (Fig. 1b). The order of trials was randomised, but the trials for filled and contour-only squares were tested in separate blocks. Each condition was repeated 9 times yielding 180 trials (5 positions of the test square x 2 directions of movement x 2 layouts of the square).

### 3.3. Results of Experiment 1A and B

Fig. 1d and e shows the average proportion of "no contact" responses across observers, plotted against the duration of the stimuli at the final position for filled and contour-only stimuli. When contact was very brief (17 ms), observers perceived a gap between the squares. The effect decreased as a function of contact duration. As shown in Fig. 1e, the effect was considerably smaller for contour-only stimuli. To quantify the effects, we conducted a generalised mixed-effect model analysis, with the binary response as the dependent variable, and the contact duration and square layout as fixed, and observers as random factors. The probability of "no contact" responses was affected by the contact duration (Chi-square(2) = 241.78, $p < 0.001$), and square layout (filled vs contour-only; Chi-square(1) = 136.7.76, $p < 0.001$). There was a significant interaction of the two factors (Chi-square(2) = 21.534, $p < 0.001$), and marginal $R^2$ was 0.42.

In a spatial position discrimination task (Experiment 1B) we tested whether the manipulation of stimulus layout (filled squares or contour-only) and the transient disappearance of stimuli affect its perceived spatial position, with the same subjects (Fig. 1b). Observers compared the final position of a moving stimulus (standard) to a spatial position of a test presented at different locations relative to the standard. To test the effect of square layout on the perceived final spatial position, we calculated the magnitude of the memory shift effect, as usually used to quantify the representational momentum (e.g. Nagai & Yagi, 2001). For each participant and condition, we summed the products of proportion "same position" responses weighted by the displacement relative to the standard stimulus' position (−0.4, −0.2, 0, 0.2 and 0.4). Then, this sum was divided by the proportion of "same position" responses. Values >0 correspond to a bias to report the test square position as displaced in the direction of motion (representational momentum), and values smaller than 0 indicate the opposite bias. The perceived displacement magnitude was tested against 0 (no representational momentum) using *t*-tests (one sided, since we tested whether the magnitude is >0). We found a tendency that this distribution was different from 0, but only for filled squares (filled: $t(15) = 1.59$, $p = 0.07$; outline only: $t(15) = 1.25$, $p = 0.16$). We observed a tendency in the direction of the representational momentum, and it is possible that certain parameters of the task, such as magnitude of the separation tested or the relatively low number of possible final vertical positions of the target in the experiment (3 only, repeated 60 times) affected the reliability of the effect. Importantly, this pattern of results cannot explain the perception of the gap between the colliding squares by an effect of the perceived spatial position of a single square.

## 4. Experiment 2: offset transients are not responsible for the apparent gap between stimuli

Offset transients of abruptly disappearing objects provide strong and unambiguous evidence about their position (Kanai, Sheth, & Shimojo, 2004; Maus & Nijhawan, 2009). They can serve as correction or reset mechanism of the motion extrapolation (Müsseler, Stork, & Kerzel, 2002), or mask the incoming information (backward masking, Breitmeyer & Kersey, 1981). Indeed, previous work showed that localising abrupt offsets of a moving stimulus can lead to underestimation of the object's final position (Maus & Nijhawan, 2009; Müsseler et al., 2002; Roulston, Self, & Zeki, 2006), and that stronger transients have a greater effect (Maus & Nijhawan, 2006). To test whether the absence of perceived contact for the brief contact duration was induced by the transient offset of the stimuli rather than predictions about the position of the moving objects, in Experiment 2 we systematically varied the separation between two abruptly disappearing squares at their final position.

### 4.1. Procedure of Experiment 2

We asked observers to compare the size of the apparent gap between two pairs of squares, in a two-interval forced choice task (2IFC). On each trial, observers were sequentially presented with two pairs of squares (~ 0 cd/m$^2$) moving towards each other on a grey background (32 cd/m$^2$) along the horizontal meridian. In separate blocks, the layout of the squares was varied: the squares were filled or represented only by their contours. In the first interval (standard), there was either physical contact between squares, or they were separated by 2.6 or 5.2 arc min at their final position. In the second interval, the squares remained on the screen for 17 or 200 ms (tested in separate blocks). In the second interval (test), we varied the size of the spatial distance between the squares. The magnitude of separation between the test pair depended on the standard separation, and was varied in seven steps. The standard squares remained on the screen for 200 ms after stopping, to avoid any uncertainty about the presented separation between them (since Experiment 1 showed that the illusion was still present at 50 ms contact in some participants). On each trial, observers responded in which interval the separation between squares appeared larger. There were twelve conditions in total (two durations of presentation of the standard at the final position, 17 or 200 ms; two layouts of squares, filled or contour-only, and the three standard separations, 0, 2.6 and 5.2 arc min), and each participant completed 588 trials.

### 4.2. Results of Experiment 2

To quantify the effects, we fitted responses with a cumulative normal distribution function, to obtain the point of the subjective equality (PSE) and subtracted from the PSEs the value of the standards. The exception was the condition in which the squares were in contact for 200 ms, since reliable fits could not be obtained. The average perceived gap and individual participants' performance for the two durations of stimuli and the two stimuli layouts are shown in Fig. 2. Individual fits are shown in the Supplementary Information.

We tested whether there was a significant overestimation of the separation between squares (different from zero) by means of Wilcoxon signed rank tests, separately for each condition (Bonferroni corrected). The overestimation was significant only in conditions in which the black squares remained at their final position for 17 ms, and only for the 0 and 2.6 arc min standard separation (e.g. when the squares were in contact for 17 ms, i.e. the 0 arc min standard separation, participants judged the separation to be greater than the separation of 2.6 arc minutes between squares remaining for 200 ms on the screen; $p < 0.001$). The bias was greater for the standard separation of 0 than 2.6 arc min (3.84(0.96) vs. 1.46(0.96) arc min; Wilcoxon paired test significant at $p < 0.001$). Strong offset transients can contribute to the perceived displacements of the final position of the squares when there is a small distance between them (2.6 arc min), but this effect should have been similar in amplitude at 0 and 2.6 arc min. The magnitude of the bias when the stimuli were in contact at their final position suggests that the apparent gap is not solely induced by the offset transients, but it depends on the distance between the two stimuli at the final position before the offset (i.e. their physical contact).

## 5. Experiment 3: opposite contrast polarity eliminates the illusion

The results of Experiments 1B and 2 suggest that the no contact illusion is not caused by an inability to process the sensory information when stimuli are presented briefly, or by a transient offset masking the sensory signal (Maus & Nijhawan, 2009; Müsseler et al., 2002; Roulston et al., 2006).

Instead, the apparent gap could be a consequence of an extrapolation of the contrast between the leading edge of the moving object and the background. Experiment 1 favours the low-level prediction interpretation, according to which local luminance patterns are extrapolated in the direction of motion (Arnold, Thompson, & Johnston, 2007; Roach et al., 2011, although see also Arnold, Marinovic, & Whitney, 2014). In Experiment 3 we verify the hypothesis that the apparent gap is a consequence of a local contrast extrapolation at the leading edge of the moving object. According to this hypothesis, when the two squares are in contact, the local contrast prediction is violated. When squares stay in brief contact (<50 ms), sensory information is combined with the prediction, yielding the percept of no contact. When objects stay in contact long enough (~50 ms), sensory information of contact is salient enough: predictions are reset, and there is a clear percept of contact between the objects. If the apparent gap between the two stimuli is indeed a consequence of the low-level prediction of luminance patterns at the leading edge of the moving objects, we would expect manipulation of their luminance and contrast relative to the background to have an effect on the apparent gap. In particular, if the apparent gap between the two squares is a consequence of a conflict between the local contrast prediction and the incoming sensory information, having two stimuli of different contrast polarity (luminance difference between the squares and the background) would diminish the effect. To test this prediction, in Experiment 3 we varied the luminance of each of the stimuli.

### 5.1. Procedure of Experiment 3

The procedure was similar to the procedure of Experiment 1A, with several modifications. The two squares appeared, at an eccentricity of 3 dva, and started moving horizontally with a constant speed (1.2 dva/s), towards the centre of the screen. When the squares stopped moving, they

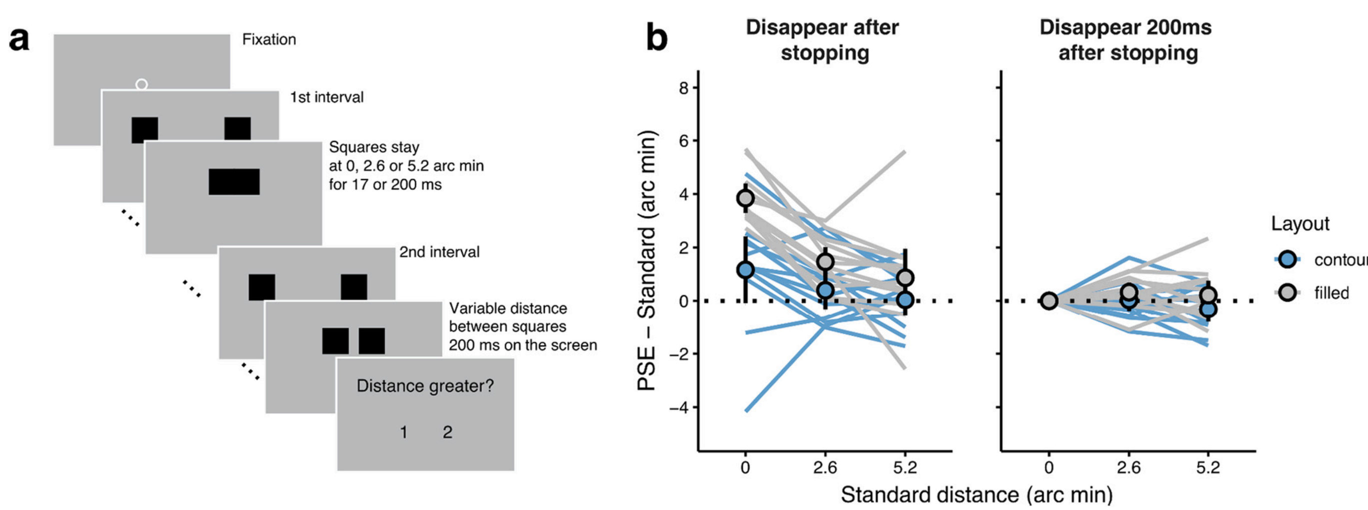


**Fig. 2.** Procedure and results of Experiment 2.
(a) Schematic representation of the stimuli sequence in Experiment 2.
(b) Results of Experiment 2. The perceived distance between the two squares as a function of standard separation, stimuli layout and duration presentation at the final position. Individual data are shown in blue and grey lines (contour-only and filled squares, respectively), and circles indicate averages across participants. When squares disappeared from the screen after stopping, the distance between them at their final position was overestimated (relative to the distance when squares remained on the screen for 200 ms, left panel). The overestimation depended on stimuli layout, and the standard separation. When the squares remained on the screen for 200 ms, no overestimation was observed (right panel). Error bars indicate standard error of the mean between participants.

remained on the screen for 17, 33, or 200 ms. Then, the squares disappeared, and observers reported whether the two squares were in contact or not (separated by 2.6 arc min, same as the smaller separation in Experiment 2), by pressing a key on a keyboard. We systematically varied the luminance of the squares in four steps (0, 23, 42, 58 cd/m$^2$, background luminance 32 cd/m$^2$). We tested all combinations of luminance pairs (four conditions in which squares had the same, and six with different luminance pairs). Different combinations were presented in a randomised order across trials. There were the same number of contact and no-contact trials, and the total number of trials was 1200 (20 repetitions × 2 contact/no contact x 3 durations × 10 luminance conditions), completed in a 2 h session, with breaks.

### 5.2. Results of Experiment 3

First, we tested the effect of luminance on the apparent gap between the squares. We analysed only conditions in which both stimuli in a trial had the same luminance, and there was no separation between squares when they contacted each other. The proportion of "no contact" responses as a function of stimuli duration at their final position for different luminances is shown in Fig. 3a-d (grey lines and empty circles). To quantify the effects, we submitted data to a generalised linear mixed-effect model analysis. The dependent variable was the binary response of participants, and the luminance and the duration of the contact were predictors. Participants were included as a random intercept. We found an effect of contact duration (Chi-square(2) = 30.346, $p$ < 0.001), luminance (Chi-square(3) = 267.4, p < 0.001) and their interaction (Chi-square(6) = 27.57, p < 0.001). The marginal R$^2$ of the model was 0.57.

Next, we tested whether the contrast polarity (whether the squares had different and opposite polarity relative to the background, or different luminance, but the same polarity) had an effect on performance. We tested a model with three predictors: the contact duration, the contrast polarity (same or different) and a variable coding whether the two stimuli had the same or different luminance (e.g. two black squares vs. one white and one black square), as well as the interaction between contact duration and the other two variables. The dependent variable was participants' binary response, and we included a random intercept at the level of participant. There was an effect of whether the two stimuli had the same luminance or not (Chi-square(1) = 200.9, $p$ < 0.001), as well as an effect of their contrast polarity (Chi-square(1) = 717.81, $p$ < 0.001). There was also an interaction between duration of contact and whether the stimuli had the same or different luminance (Chi-square(2) = 34.25, p < 0.001), and the duration of contact and the contrast polarity (Chi-square(2) = 46.52, p < 0.001). The marginal R$^2$ of the model was 0.414. Comparing this model to the model that did not include contrast polarity, we found that the full model provided a better fit to the data (AIC$_{full}$ = 6062.4 and AIC$_{no\ polarity}$ = 6968.45).

Interestingly, varying contrast polarity also had an effect on the ability to detect the physical separation between stimuli on those trials in which squares were not in contact (Fig. 4). There was a significant effect of the polarity on the ability to detect separation (Chi-square(1) = 648.73, p < 0.001), as well as effect of the contact duration (Chi-square (2) = 104.5, p < 0.001), but no interaction between the two factors (Chi-square(2) = 3.45, $p$ = 0.18), the model's marginal R$^2$ was 0.478.

In summary, we found that when the contrast polarity of the two squares relative to the background is in the opposite direction (e.g. a white and a black square on a mid-grey background), the percept of a gap is eliminated (Fig. 4c-f). This result was observed despite the fact that the difference in luminance between the two squares was similar in opposite and same-polarity conditions, that is, with a similar contrast at the edge between the squares when they contact each other. This indicates the importance of background luminance in addition to the squares' luminance. In addition, gap detection was impaired for all opposite contrast polarity stimuli, as shown in Fig. 4. In these conditions, the apparent gap between the two stimuli is ambiguous, possibly because the local prediction interferes with contrast and edge ownership detection (Zhou, Friedman, & Von Der Heydt, 2000). Nevertheless, as shown in Fig. 4c-f, the time course of this effect is different than that of the apparent gap between the squares, since it persists even for 200 ms of contact between the squares. Furthermore, there was a very low consensus between participants.

Predictive coding and representational momentum are not the only hypotheses explaining motion-induced position shifts. Response gain modulation by lateral interactions between motion sensitive neurons also modulates motion perception (Arnold et al., 2007; Berry et al.,

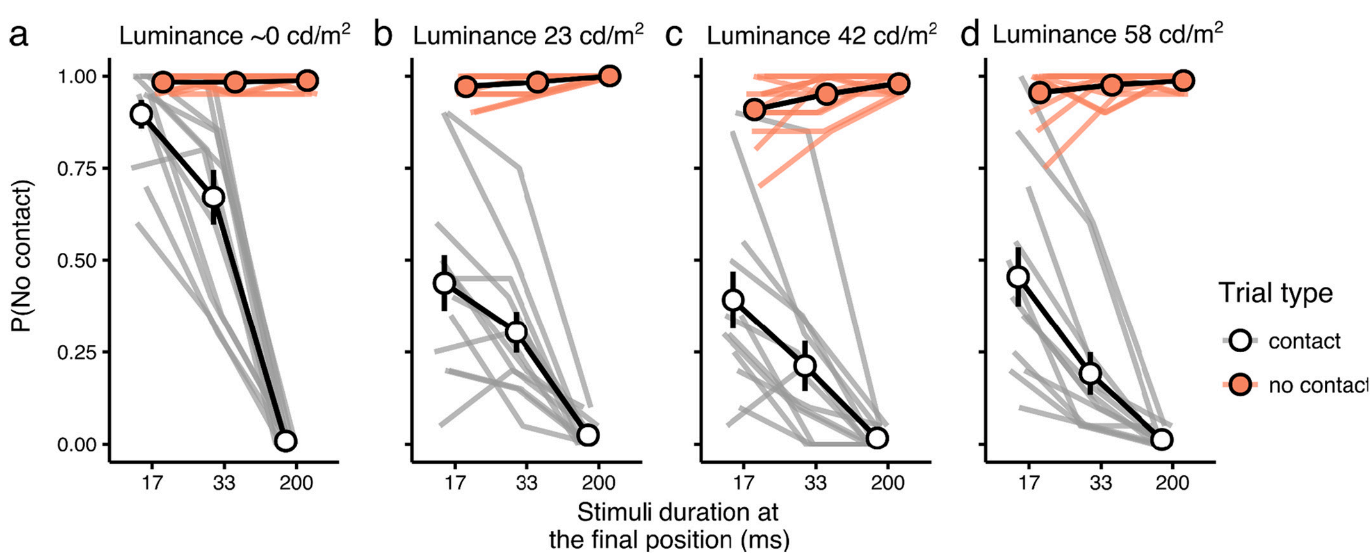


**Fig. 3.** Results of Experiment 3.
(a-d) The proportion of "no contact" responses is shown against the three stimuli durations at the final position, for trials in which the squares contacted (white symbols and grey lines) or not (orange symbols and lines). The four luminance conditions are shown in separate panels (0, 23, 42 and 58 cd/m$^2$). Individual performance is shown with grey and orange lines, and mean data with circles. When squares were in physical contact before disappearing, the apparent gap was perceived most frequently when the black squares (panel a) stayed in contact for 17 ms. The apparent gap was perceived less frequently for squares with higher luminances (b-d). In trials in which there was a physical gap between the squares (orange symbols) it was correctly detected. Error bars indicate the standard error of the mean.

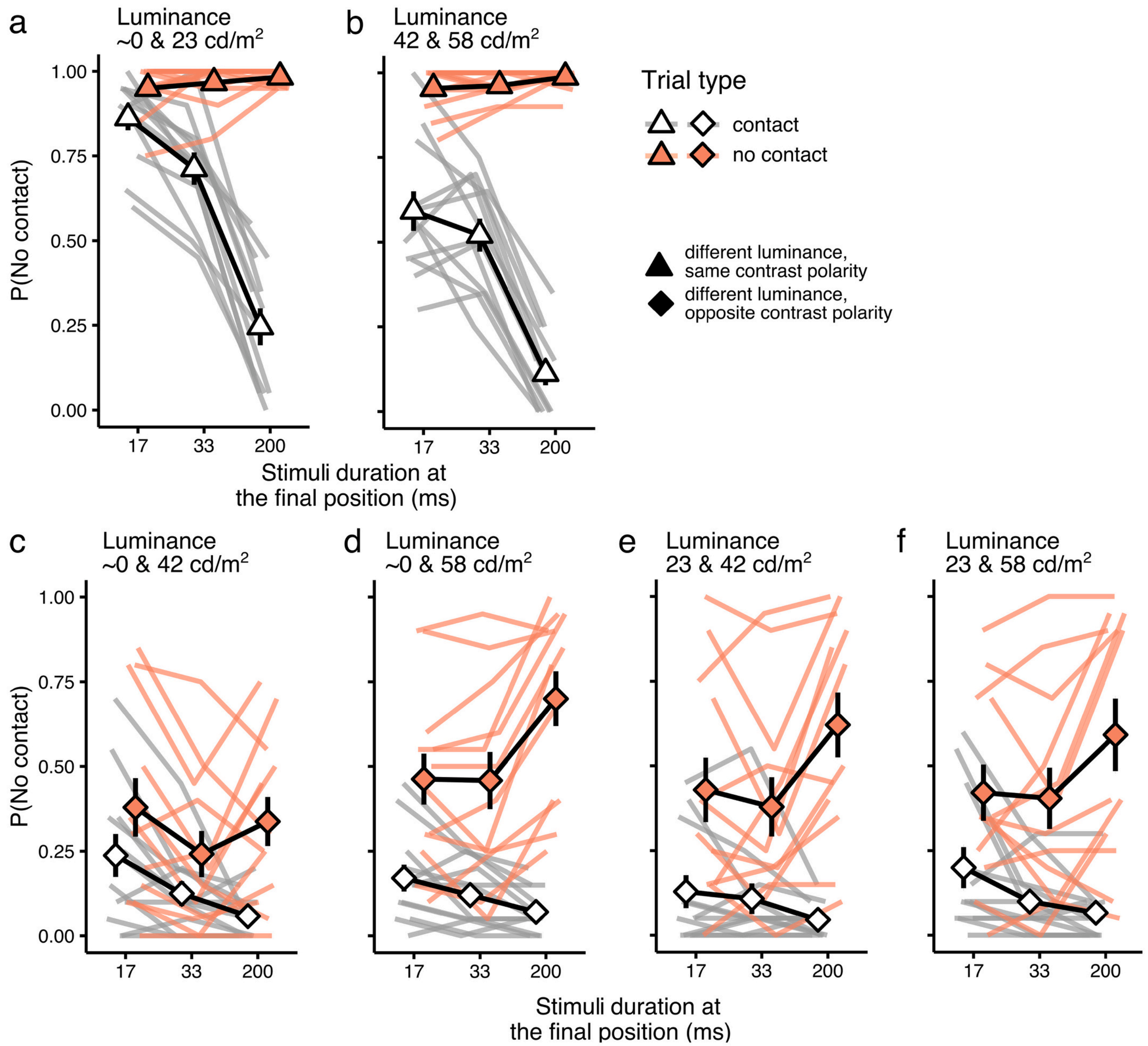


**Fig. 4.** Effect of contrast polarity on detection of contact.
(a-f) The proportion of "no contact" responses as a function of the stimuli durations at the final position, for trials in which the squares contacted (white symbols and grey lines) or not (orange symbols and lines). Individual performance is shown with grey and orange lines, and mean data with circles. The six combinations of squares' luminance is shown in separate panels. Error bars indicate the standard error of the mean.
(a-b) The proportion of "no contact" responses for the squares with the same contrast polarity conditions. When the two squares had different luminance, but same contrast polarity (both were either lighter or darker than the background), participants perceived a gap between the squares when squares briefly contacted (17 ms; grey lines and open symbols). In contrast, when there was no physical contact between the squares, the separation was correctly detected (high proportion of "no contact" responses, orange lines and symbols).
(c-f) The proportion of "no contact" responses for the squares with the opposite contrast polarity conditions. When the two squares had different contrast polarity relative to the background, participants correctly detected the contact between the squares (low proportion of "no contact" responses; grey lines and open symbols). In contrast, the physical separation between the two squares with the opposite contrast polarity was ambiguous (orange lines and symbols).

1999). In salamander and rabbit retinae, a moving stimulus induces anticipatory activity in ganglion cells. This activity is greater for large contrasts, and asymmetrical with respect to the leading/trailing edge of the motion (Berry et al., 1999). This activity is direction independent, and possibly when there are two stimuli moving towards one another the gain control starts earlier, and even earlier for high contrast stimuli, resulting in the attenuation of signals at the point of contact. This hypothesis would explain the smaller effect found for the low-contrast stimuli in Experiment 3. In addition, contrast affects the perceived speed of movement of the stimulus, and a low-contrast drifting stimulus can appear up to 50% slower than a high contrast one (Anstis, 2003; Stone & Thompson, 1992). This hypothesis can be tested by varying speed of stimulus movement, since for faster moving stimuli the gain control mechanism should be less active (Berry et al., 1999).

## 6. Experiment 4: faster speed of stimulus movement does not reduce the apparent gap

To test whether the speed of stimulus movement affects the illusion, we presented observers with the squares moving towards each other, and varied their movement speed from trial to trial. This manipulation allowed us to test the possibility that the apparent gap is related to gain modulation mechanisms, as suggested by the fact that the illusion is larger for black than grey squares in Experiment 3.

### 6.1. Procedure of Experiment 4

The procedure was similar to the procedure of Experiment 1A with several modifications. The two black squares appeared, at eccentricity of 3 dva, and started moving horizontally with a constant speed on a grey background (32 cd/m$^2$). In Experiment 4, their movement speed was varied from trial to trial (0.6, 1.2, 2.4 dva/s). When the squares stopped moving, they remained on the screen for 17, 33, or 50 ms. There was either no separation between the squares at the final position, or they were separated by 2.6 arc min (as in Experiments 2 and 3). Then, the squares disappeared, and observers reported whether the two squares were in contact or not. We obtained 20 repetitions for each of the contact conditions (20 repetitions $\times$ 3 speeds $\times$ 3 contact durations) and 20 repetitions for each of the no-contact conditions (20 repetitions $\times$ 3 speeds $\times$ 1 duration), yielding 240 trials in total. Trials with different movement speeds were presented in a randomised order.

### 6.2. Results of Experiment 4

The average proportion of "no contact" responses across observers is plotted against the speed of stimulus movement in Fig. 5. Performance for the different durations of the stimuli at their final position is shown in different panels. To test the effect of speed of stimulus movement on the perceived separation, we submitted the responses to generalised mixed-effect model analysis. The dependent variable was the binary response, and predictors were the duration of contact and speed of stimulus movement, with observers as a random effect. We analysed only trials in which there was a physical contact between the squares, given the ceiling performance in the "no contact" condition (orange symbols in Fig. 5). We found an effect of the duration of contact (Chi-square (2) = 255.54, $p < 0.01$), but there was no effect of speed of stimulus movement (Chi-square (2) = 1.13, $p = 0.56$) or their interaction (Chi-square (4) = 3.51, $p = 0.48$), and $R^2$ of the model was 0.35.

We found that the speed of stimulus movement did not affect the apparent gap between the squares: there was no significant effect of displacement speed on the proportion of "no contact" responses. These findings are inconsistent with the local gain control hypothesis, which would predict a decrease in the percept of the gap with increasing speed of stimulus movement (Arnold et al., 2007; Berry et al., 1999).

## 7. Discussion

We presented a compelling illusion of the apparent gap between moving objects at the end of their trajectory, which occurs when the leading edges of those objects contact only briefly. The illusion was present when two stimuli move towards each other, though individual stimuli were not misperceived as disappearing in a backwards displaced position (Fig. 1f and g). In subsequent experiments, we showed that the effect is not a consequence of an inability to process briefly presented sensory information, a transient offset masking the sensory signal (Maus & Nijhawan, 2006, 2009; Müsseler et al., 2002; Roulston et al., 2006), or a local gain control mechanism (Arnold et al., 2007; Berry et al., 1999).

When two objects move towards each other, an intuitive expectation is that they will contact. Remarkably, this was not what observers reported: we found a strong and robust percept of a gap between the two objects. In Experiment 2, participants performed a different task: they were asked to compare the size of the perceived gap between the two pairs of squares. The results showed that the perceived size of the gap for the two squares who contacted briefly was disproportionately greater than that in other conditions, suggesting a genuine percept rather than a decision bias. This illusion can be explained as a consequence of violation of specific low-level predictions, independent of high-level expectations. According to the predictive coding scheme, when predictions are violated, the error signal is propagated across the prediction loop. Consequently, the final percept is a combination of the erroneous prediction and incoming sensory information (Kok & de Lange, 2015; Rao & Ballard, 1999). When an object is moving, its position is extrapolated and the future position predicted across the prediction loop (Khoei, Masson, & Perrinet, 2017; Roach et al., 2011). Low-level local predictions, in the form of an edge or figure-ground contrast extrapolation (Hesse & Tsao, 2016; Peterhans & Von Der Heydt, 1989; Von Der Heydt & Peterhans, 1989) in spatial proximity of the leading edge of the squares, could lead to a conflict between predicted local contrast edge and incoming information (contact between squares and change in contrast: no edge between squares in Experiments 1A, 2 and 4, edge but change in contrast polarity between squares in Experiment 3). This

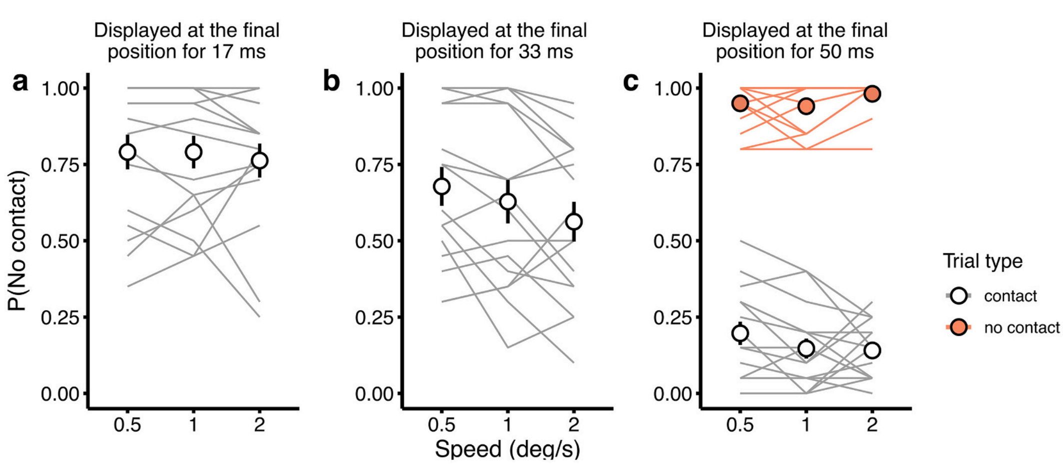


**Fig. 5.** Effect of the speed of stimulus movement. (a-c) The proportion of "no contact" responses is plotted against the speed of stimulus movement. The three different durations of the squares' presentation at the final position is shown in panels a-c (17, 33, and 50 ms, respectively). Grey lines indicate individual performance, and averages are shown in circles. In panel c, orange symbols indicate the performance in trials in which there was no contact between the squares. Error bars indicate standard error of the mean. There was an effect of contact duration, and the gap was perceived between stimuli that were presented on the screen for 17 and 33 ms. There was no evidence supporting the effect of the speed of stimulus movement on the magnitude of the apparent gap.

conflict between the forward prediction and incoming sensory information takes time to be resolved, and the erroneous percept persists for ~50 ms. On the other hand, when a single moving stimulus is presented (Experiment 1B, representational momentum, e.g. Freyd & Finke, 1984; Hubbard & Ruppel, 2014) no backward displacement is found (although see Hubbard & Bharucha, 1988 and Verfaillie & d'Ydewalle, 1991). Similarly, when the distance between the two squares is large (Experiment 2), the illusion is diminished to the point of being negligible. In other words, when there is no conflict between the forward prediction and the incoming information, there is no reliable apparent gap between squares. Importantly, it is not the prediction of the future position of the squares that affects the percept of the gap. In fact, it is probable that given the repetition of trials, participants expect the squares to stop when they reach the middle of the screen. What seems to be at stake here is the prediction of the square-background contrast.

By varying the luminance of stimuli, we showed that the illusion persists even when the two squares have different luminances, so long as they both have the same contrast polarity relative to the background. This finding is important, because it indicates that the effect persists even when there is a clear luminance edge between the two objects at the time of contact. The systematic manipulation of the squares' luminance in Experiment 3 shows that the same difference in luminance between the squares can lead to radically different percepts, despite the presence of a luminance contrast between the squares when they contact. This finding confirms the importance of the background luminance, supporting the hypothesis of the contrast extrapolation at the leading edge of the moving objects, rather than an effect of the mere presence of a separation cue between the squares. Interestingly, the illusion was eliminated with opposite contrast polarity of the two squares relative to the background.

The work reported here allows us to discard a number of additional alternative explanations. Different perceived offset time of the high and low luminance stimuli is unlikely to eliminate the percept of the gap, since the perceived synchrony between two abutting stimuli is only slightly affected by the difference in their luminances (Allik & Kreegipuu, 1998). The effect of contrast polarity is reminiscent of paracontrast masking, where opposite contrast polarity between the target and the mask leads to facilitation instead of inhibition of target visibility (Kafaligönül, Breitmeyer, & Öğmen, 2009). That said, if masking were responsible for the effect, by reducing the visibility of the stimuli at their final position, we would expect reduced visibility of both squares that were briefly in contact as well as those that stopped moving before their leading edges contacted. In contrast, the results of Experiment 2 suggest that is not the case, showing that the percept depends on the contact between stimuli. Furthermore, Experiment 2 confirms that results of Experiment 1 are not a consequence of inability to perceive very brief contacts. In particular, the separation between the squares that contacted for 17 ms was perceived as greater than the separation between squares that were separated by 2.6 arc min and remained on the screen for 200 ms.

Experiment 2 also allows us to discard the hypothesis of the attentional repulsion effect: perceived position of stimuli can be biased away from positions previously cued (e.g. Kosovicheva, Fortenbaugh, & Robertson, 2010; Suzuki & Cavanagh, 1997). The apparent displacement could be a consequence of participants' attention directed to the position on the screen where the squares stopped, and their perceived final position displaced away from the focus of attention. However, the spatial profile of the attentional repulsion is different from that of the effect we report here. In particular, the magnitude of the attentional repulsion effect increases when the distance between the cue and the target increases up to 2° (Kosovicheva et al., 2010), while results of Experiment 2 showed that the apparent gap between the squares was largest when the two squares were in contact, and decreased as they were further away from each other. Of course, it is still possible that there is an alternative explanation for the pattern of results we observed, which is to be addressed in the future work.

It should be noted that there was high uncertainty in estimations about the contact between squares with opposite contrast polarity, in conditions in which there was a physical separation between them (Fig. 4). This finding is in general agreement with previous work showing impaired position acuity for objects with opposite contrast polarity features, although it is not clear why a mechanism impairing spatial judgements of opposite contrast polarity features would lead to veridical contact percept of opposite contrast polarity squares (Levi, Jiang, & Klein, 1990; Levi & Waugh, 1996). The results are rather consistent with a role for low-level contrast prediction: if the forward model extrapolates the contrast of the leading edge, the extrapolation of contrast of the opposite contrast polarity squares should not lead to a conflict, since the predicted contrast gradient is preserved when they contact.

We also found that the illusion effect increased with greater contrast between the stimuli and the background, at least when the squares were black (Hubbard & Ruppel, 2014). Smaller effects for low contrast stimuli could be a consequence of an adaptive change in spatial summation at low contrast (Sceniak, Ringach, Hawken, & Shapley, 1999) or a difference in the response profile in early visual cortex (Albrecht, 1995; Albrecht, Geisler, Frazor, & Crane, 2002; Goodyear & Menon, 1998).

There is a great body of evidence showing neural activity consistent with the predictive coding scheme (e.g. Blom et al., 2020; Todorovic & de Lange, 2012; Wacongne et al., 2011), but evidence for local sensory predictions is scarce (Roach et al., 2011; Van Humbeeck et al., 2016), and whether their violations have perceptual consequences is unknown. We suggest that the compelling effect we report here is a demonstration of the predictive mechanisms at the perceptual level. The illusion shows the consequences of the violation of specific, low-level predictions, offering a versatile tool for investigating predictive mechanisms at the sensory level in different populations. The impaired temporal predictions of schizophrenia patients have been related to a specific set of symptoms, and this paradigm offers a tool to investigate putative impairments at the early stages of sensory information processing (Marques-Carneiro, Krieg, Duval, Schwitzer, & Giersch, 2021; Martin et al., 2017).

## CRediT authorship contribution statement

**Ljubica Jovanovic:** Conceptualization, Investigation, Formal analysis, Software, Visualization, Writing – original draft. **Mélanie Trichanh:** Investigation. **Brice Martin:** Conceptualization, Methodology. **Anne Giersch:** Conceptualization, Formal analysis, Software, Supervision, Writing – review & editing.

## Data availability

All data and demos are available at https://osf.io/f27sc/

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## Appendix A. Supplementary data

All data and demos are available at https://osf.io/f27sc/.Supplementary data to this article can be found online at [https://doi.org/10.1016/j.cognition.2022.105279].

## References

Albrecht, D. G. (1995). Visual cortex neurons in monkey and cat: Effect of contrast on the spatial and temporal phase transfer functions. *Visual Neuroscience, 12*(6), 1191–1210.

Albrecht, D. G., Geisler, W. S., Frazor, R. A., & Crane, A. M. (2002). Visual cortex neurons of monkeys and cats: Temporal dynamics of the contrast response function. *Journal of Neurophysiology, 88*(2), 888–913.
Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *The Journal of Neuroscience, 30*(8), 2960–2966. https://doi.org/10.1523/JNEUROSCI.3730-10.2010
Allik, J., & Kreegipuu, K. (1998). Multiple visual latency. *Psychological Science, 9*(2), 21–24.
Anstis, S. (2003). Moving objects appear to slow down at low contrasts. *Neural Networks, 16*(5–6), 933–938.
Arnold, D. H., Marinovic, W., & Whitney, D. (2014). Visual motion modulates pattern sensitivity ahead, behind, and beside motion. *Vision Research, 98*, 99–106. https://doi.org/10.1016/j.visres.2014.03.003
Arnold, D. H., Thompson, M., & Johnston, A. (2007). Motion and position coding. *Vision Research, 47*(18), 2403–2410. https://doi.org/10.1016/j.visres.2007.04.025
Aru, J., Tulver, K., & Bachmann, T. (2018). It's all in your head: Expectations create illusory perception in a dual-task setup. *Consciousness and Cognition, 65*, 197–208.
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48.
Benvenuti, G., Chemla, S., Boonman, A., Perrinet, L., Masson, G. S., & Chavane, F. (2020). *Anticipatory responses along motion trajectories in awake monkey area V1* (BioRxiv).
Berry, M. J., Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature, 398*(6725), 334–338.
Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience, 1*(7), 635–640.
Blom, T., Feuerriegel, D., Johnson, P., Bode, S., & Hogendoorn, H. (2020). Predictions drive neural representations of visual events ahead of incoming sensory information. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1917777117, 201917777.
Breitmeyer, B. G., & Kersey, M. (1981). Backward masking by pattern stimulus offset. *Journal of Experimental Psychology. Human Perception and Performance, 7*(5), 972–977.
Brenner, E., & Smeets, J. B. J. (2000). Motion extrapolation is not responsible for the flash – Lag effect. *Vision Research, 40*, 1645–1648.
Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255*(5040), 90–92.
Ekman, M., Kok, P., & de Lange, F. P. (2017). Time-compressed preplay of anticipated events in human primary visual cortex. *Nature Communications, 8*(1), 1–9.
Freyd, J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 10*(1), 126–132.
Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 360*, 815–836. https://doi.org/10.1098/rstb.2005.1622
Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience, 21*(20). RC172-RC172.
Goodyear, B. G., & Menon, R. S. (1998). Effect of luminance contrast on BOLD fMRI response in human primary visual areas. *Journal of Neurophysiology, 79*(4), 2204–2207.
Hesse, J. K., & Tsao, D. Y. (2016). Consistency of border-ownership cells across artificial stimuli, natural stimuli, and stimuli with ambiguous contours. *Journal of Neuroscience, 36*(44), 11338–11349. https://doi.org/10.1523/JNEUROSCI.1857-16.2016
Hogendoorn, H. (2020). Motion extrapolation in visual processing: Lessons from 25 years of flash-lag debate. *The Journal of Neuroscience, 40*(30), 5698–5705.
Hogendoorn, H., Carlson, T. A., & Verstraten, F. A. J. (2008). Interpolation and extrapolation on the path of apparent motion. *Vision Research, 48*(7), 872–881. https://doi.org/10.1016/j.visres.2007.12.019
Houde, J. F., Nagarajan, S. S., Sekihara, K., & Merzenich, M. M. (2002). Modulation of the auditory cortex during speech: An MEG study. *Journal of Cognitive Neuroscience, 14*(8), 1125–1138.
Hubbard, T. L. (2005). Representational momentum and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin & Review, 12*(5), 822–851.
Hubbard, T. L. (2019). Momentum-like effects and the dynamics of perception, cognition, and action. *Attention, Perception, & Psychophysics, 81*(7), 2155–2170.
Hubbard, T. L., & Bharucha, J. J. (1988). Judged displacement in apparent vertical and horizontal motion. *Perception & Psychophysics, 44*(3), 211–221.
Hubbard, T. L., & Ruppel, S. E. (2014). An effect of contrast and luminance on visual representational momentum for location. *Perception, 43*(8), 754–766. https://doi.org/10.1068/p7714
Jancke, D., Erlhagen, W., Dinse, H. R., Akhavan, A. C., Giese, M., Steinhage, A., & Schöner, G. (1999). Parametric population representation of retinal location: Neuronal interaction dynamics in cat primary visual cortex. *Journal of Neuroscience, 19*(20), 9016–9028.
Kafaligönül, H., Breitmeyer, B. G., & Öğmen, H. (2009). Effects of contrast polarity in paracontrast masking. *Attention, Perception, & Psychophysics, 71*(7), 1576–1587.
Kanai, R., Sheth, B. R., & Shimojo, S. (2004). Stopping the motion and sleuthing the flash-lag effect: Spatial uncertainty is the key to perceptual mislocalization. *Vision Research, 44*(22), 2605–2619.
Kerzel, D., & Gegenfurtner, K. R. (2003). Neuronal processing delays are compensated in the sensorimotor branch of the visual system. *Current Biology, 13*(22), 1975–1978.
Khoei, M. A., Masson, G. S., & Perrinet, L. U. (2017). The flash-lag effect as a motion-based predictive shift. *PLoS Computational Biology, 13*(1), Article e1005068.
Kok, P., & de Lange, F. P. (2015). Predictive coding in sensory cortex. In *An introduction to model-based cognitive neuroscience* (pp. 221–244). New York, NY: Springer.
Kok, P., Failing, M. F., & de Lange, F. P. (2014). Prior expectations evoke stimulus templates in the primary visual cortex. *Journal of Cognitive Neuroscience, 26*(7), 1546–1554. https://doi.org/10.1162/jocn
Kosovicheva, A. A., Fortenbaugh, F. C., & Robertson, L. C. (2010). Where does attention go when it moves?: Spatial properties and locus of the attentional repulsion effect. *Journal of Vision, 10*(12), 33:1–13.
Leptourgos, P., Bouttier, V., Jardri, R., & Denève, S. (2020). A functional theory of bistable perception based on dynamical circular inference. *PLoS Computational Biology, 16*(12), Article e1008480.
Levi, D., Jiang, B.-C., & Klein, S. (1990). Spatial interval discrimination with blurred lines: Black and white are separate but not equal at multiple spatial scales. *Vision Research, 30*(11), 1735–1750.
Levi, D., & Waugh, S. (1996). Position acuity with opposite-contrast polarity features: Evidence for a nonlinear collector mechanism for position acuity ? *Vision Research, 36*(4), 573–588.
Linares, D., & López-Moliner, J. (2016). quickpsy: An R package to fit psychometric functions for multiple groups. *The R Journal, 8*(1), 122–131.
MacKay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature, 181*(4607), 507–508.
Marques-Carneiro, J. E., Krieg, J., Duval, C. Z., Schwitzer, T., & Giersch, A. (2021). Paradoxical sensitivity to sub-threshold asynchronies in schizophrenia: A behavioural and EEG approach. *Schizophrenia Bulletin Open, 2*(1), sgab011.
Martikainen, M. H., Kaneko, K., & Hari, R. (2005). Suppressed responses to self-triggered sounds in the human auditory cortex. *Cerebral Cortex, 15*(3), 299–302. https://doi.org/10.1093/cercor/bhh131
Martin, B., Franck, N., Cermolacce, M., Falco, A., Benair, A., Etienne, E., Weibel, S., Coull, J. T., & Giersch, A. (2017). Fragile temporal prediction in patients with schizophrenia is related to minimal self disorders. *Scientific Reports, 7*(1), 1–10.
Maus, G. W., Fischer, J., & Whitney, D. (2013). Motion-dependent representation of space in area MT+. *Neuron, 78*(3), 554–562.
Maus, G. W., & Nijhawan, R. (2006). Forward displacements of fading objects in motion: The role of transient signals in perceiving position. *Vision Research, 46*(26), 4375–4381.
Maus, G. W., & Nijhawan, R. (2009). Going, going, gone: Localizing abrupt offsets of moving objects. *Journal of Experimental Psychology: Human Perception and Performance, 35*(3), 611–626. https://doi.org/10.1037/a0012317
Muckli, L., Kohler, A., Kriegeskorte, N., & Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology, 3*(8), 1501–1510. https://doi.org/10.1371/journal.pbio.0030265
Müsseler, J., Stork, S., & Kerzel, D. (2002). Comparing mislocalizations with moving stimuli : The Fröhlich effect, the flash-lag, and representational momentum. *Visual Cognition, 9*(1–2), 120–138. https://doi.org/10.1080/13506280143000359
Nagai, M., & Yagi, A. (2001). The pointedness effect on representational momentum. *Memory & Cognition, 29*(1), 91–99.
Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133–142.
Peterhans, E., & Von Der Heydt, R. (1989). Mechanisms of contour perception contours bridging gaps in monkey visual cortex. II. Contours bridging gaps. *The Journal of Neuroscience, 9*(5), 1749–1763.
Pins, D., & Ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral Cortex, 13*(5), 461–474.
Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience, 2*(1), 79–87.
Roach, N. W., McGraw, P. V., & Johnston, A. (2011). Visual motion induces a forward prediction of spatial pattern. *Current Biology, 21*(9), 740–745. https://doi.org/10.1016/j.cub.2011.03.031
Roulston, B. W., Self, M. W., & Zeki, S. (2006). Perceptual compression of space through position integration. *Proceedings of the Royal Society, 273*(1600), 2507–2512. https://doi.org/10.1098/rspb.2006.3616
Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience, 2*(8), 733–739.
Schellekens, W., van Wezel, R. J. A., Petridou, N., Ramsey, N. F., & Raemaekers, M. (2016). Predictive coding for motion stimuli in human early visual cortex. *Brain Structure and Function, 221*(2), 879–890. https://doi.org/10.1007/s00429-014-0942-2
Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research, 32*(8), 1535–1549.
Sundberg, K. A., Fallah, M., & Reynolds, J. H. (2006). A motion-dependent distortion of retinotopy in area V4. *Neuron, 49*(3), 447–457.
Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: An attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance, 23*(2), 443.
Todorovic, A., & de Lange, F. P. (2012). Repetition suppression and expectation suppression are dissociable in time in early auditory evoked fields. *The Journal of Neuroscience, 32*(39), 13389–13395. https://doi.org/10.1523/JNEUROSCI.2227-12.2012
Van Humbeeck, N., Putzeys, T., & Wagemans, J. (2016). Apparent motion suppresses responses in early visual cortex: A population code model. *PLoS Computational Biology, 12*(10), Article e1005155.
Verfaillie, K., & d'Ydewalle, G. (1991). Representational momentum and event course anticipation in the perception of implied periodical motions. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 17*(2), 302.

Von Der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *The Journal of Neuroscience, 9*(5), 1731–1748.
Wacongne, C., Labyt, E., van Wassenhove, V., Bekinschtein, T., Naccache, L., & Dehaene, S. (2011). Evidence for a hierarchy of predictions and prediction errors in human cortex. *Proceedings of the National Academy of Sciences, 108*(51), 20754–20759.
Zhou, H., Friedman, H. S., & Von Der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience, 20*(17), 6594–6611. https://doi.org/10.1523/jneurosci.20-17-06594.2000