



Strikingly rapid neural basis of motion-induced position shifts revealed by high temporal-resolution EEG pattern classification



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ABSTRACT

Several visual illusions demonstrate that the neural processing of visual position can be affected by visual motion. Well-known examples are the flash-lag, flash-drag, and flash-jump effect. However, where and when in the visual processing hierarchy such interactions take place is unclear. Here, we used a variant of the flash-grab illusion (*Vision Research* 91 (2013), pp. 8–20) to shift the perceived positions of flashed stimuli, and applied multivariate pattern classification to individual 64-channel EEG trials to dissociate neural signals corresponding to veridical versus perceived position with high temporal resolution. We show illusory effects of motion on perceived position in three separate analyses: (1) A classifier can distinguish different perceived positions of a flashed object, even when the veridical positions are identical. (2) When the perceived positions of two objects presented in different locations become more similar, the classifier performs less well than when they become more different, even if the veridical positions remain unchanged. (3) Finally, a classifier can discriminate the perceived position of an object even when trained on objects presented in physically different positions. These effects are evident as early as 81 ms post-stimulus, concurrent with the very first EEG signals indicating that any stimulus is present at all. This finding shows that the illusion must begin at an early level, probably as part of a predominantly feed-forward mechanism, leaving the influence of any recurrent processes to later stages in the development of the effect.

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1. Introduction

A range of visual illusions demonstrate that neural processing of motion and position interact. For example, in the Fröhlich effect (Fröhlich, 1923), the initial position of a moving object seems shifted along its trajectory. Similarly, when a stimulus is flashed next to a moving object, the flash appears to lag behind the moving object (the flash-lag effect; Nijhawan, 1994). A flash presented adjacent to a moving texture is shifted in the direction of motion of the moving texture (the flash-drag effect; Whitney & Cavanagh, 2000a, 2000b), and the perceived position of a stationary patch containing a moving texture appears shifted in the direction of its internal motion (e.g. Anstis, 1989; De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Finally, transient changes in a moving object's size or color are perceived to occur further along

the object's trajectory (Cai & Schlag, 2001), and reversing a moving object's direction of motion shifts the perceived location of a concurrently presented flash along the object's new trajectory (the flash-grab effect; Cavanagh & Anstis, 2013). Eagleman and Sejnowski (2007) presented a unified explanation of these phenomena, making a compelling case that instantaneous localization judgments of a flashed object are affected by motion signals collected over a roughly 80 ms period following initial detection of the object. Being based purely on psychophysical data, their model did little to address the neural architecture underlying this putative mechanism. However, the proposed retroactive nature of the effect of motion on perceived position, together with the relatively long integration window, imply a relatively late locus of interaction.

This notion is at odds with a number of neurophysiological studies that demonstrate motion–position interactions at a very early stage of visual processing, at the level of the primary visual cortex or before in the visual processing hierarchy. In salamanders and rabbits, receptive fields in retinal ganglion cells shift toward the future position of a moving object (Berry et al., 1999;

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Schwartz et al., 2007). Similarly, thalamic relay cells in cat LGN show feature-specific synchronization in response to moving contours, pre-activating cell populations coding for the future position of a moving object (Sillito et al., 1994). Indeed, receptive fields in cat V1 shift to anticipate the arrival of a moving object, such that the peak population activity occurs at a shorter latency when a stimulus moves smoothly into the population's receptive field than when it is flashed there (Jancke et al., 2004). Finally, the tilt-aftereffect, thought to depend on adaptation of V1 cells (Movshon & Lennie, 1979), can be shifted by motion-induced position shifts (Kosovicheva et al., 2012). Together, these studies suggest that motion and position information start interacting very early in visual processing, already before visual information first reaches the cerebral cortex, and that subsequent feedback connections between cortical areas are not necessary to cause motion-induced position shifts.

However, other evidence suggests that the neural interactions underlying motion-induced position shifts only take place further along the visual processing pathway. For example, Maus, Fischer, and Whitney (2013) found that in areas V3A and MT (but not in V1–V3), patterns of fMRI activity evoked by stimuli whose perceived position was shifted due to the flash-drag illusion were similar to patterns of activity evoked by stimuli physically presented in those locations. The observation that disrupting activity in area MT by transcranial magnetic stimulation (TMS) reduces motion-induced position illusions also suggests that area MT contributes critical information to the interaction (Maus, Fischer, & Whitney, 2013; McGraw, Walsh, & Barrett, 2004). Finally, motion-induced mislocalization can be modulated by attention (Tse et al., 2011), and is reduced in the absence of attention to individual motion trajectories (Cavanagh & Anstis, 2013; Linares & Lopez-Moliner, 2007). These findings therefore suggest the involvement of higher-level processes, implicating later visual cortical areas as possible sites of interaction and also suggesting that feedback connections between visual cortical areas are necessary to cause motion-induced position shifts.

As such, there is evidence for both early and late motion–position interactions. Unfortunately, because the time–course of neural processing in motion–position interactions has not been studied, it has not yet been possible to identify contributions from early, feed-forward responses from later feedback processes. Here, we use the flash-grab illusion (Cavanagh & Anstis, 2013) to shift the apparent location of flashed objects, and apply multivariate pattern classification to high temporal resolution electro-encephalography (EEG) recordings to directly compare patterns of neural activation over time. We show that illusory motion–position interactions are already evident in the very first cortical response to the stimulus. This indicates that the illusion must begin at an early level of processing, probably as part of a predominantly feed-forward mechanism, leaving the influence of any recurrent processes to later stages in the development of the effect.

2. Methods

2.1. Observers

Ten observers participated in the experiment (age 19–28). All observers had normal or corrected-to-normal vision and gave informed consent prior to participation. All work was carried out in accordance with the declaration of Helsinki.

2.2. Stimulus and procedure

The stimulus was presented on an 18" Dell Trinitron monitor at 1280 × 1024 resolution with 100 Hz refresh rate at a distance of

approximately 100 cm, controlled by a PC running Matlab 7.01 with Psychtoolbox 2.54 extensions (Brainard, 1997; Pelli, 1997).

The stimulus consisted of an annulus composed of 18 alternating black and white segments, presented on a gray background at 75% of maximum monitor contrast. Inner and outer radii of the annulus were 9.3 deg and 13.7 deg of visual angle, respectively. A fixation point was presented at the center of the display.

The annulus rotated at a continuous angular velocity of 200 deg/s, repeatedly reversing direction after a variable delay (1000, 1100, 1200, 1300, 1400, or 1500 ms).

On 75% of reversals, a small colored disc (diameter 3.12 deg) was presented for a single frame (10 ms) exactly at the moment of reversal, superimposed on the annulus at a radius of 11.5 deg from fixation. There were three possible positions of the disc: 160 deg, 180 deg, or 200 deg of polar angle offset from the top of the annulus. The disc was always presented centered on an edge between black and white segments of the annulus. Fig. 1 shows the possible locations of the disc. Stimulus parameters were set on the basis of pilot experiments in a separate group of observers, such that the average size of the flash-grab effect was half of the distance separating possible locations of the disc. In this way, two discs presented in adjacent locations (e.g. I and II) could be made to appear in the same position (i.e. B) using the illusion. Observers in the current experiment were not asked to report the perceived position to avoid making position a task-relevant feature.

On 83.3% of trials on which a disc was presented, the disc was bright red. On the remaining 16.7% of trials, the disc was instead bright green. These green discs served as targets, to which observers were instructed to respond with a keypress. Observers were not required to respond to red discs. The location of the disc was task-irrelevant, and only trials with red discs were included in the final analysis. Observers were briefly familiarized with the stimulus and the task before the experiment; during the experiment, observers missed very few targets (all observers 2 or fewer) and no false alarms were made at all.

The stimulus was presented in 24 blocks of just under 7 min each, divided over two sessions on different days. Each block consisted of a total of 288 reversals.

2.3. EEG acquisition and analysis

During all trials, 64-channel EEG was acquired at a sampling rate of 2048 Hz. Data were resampled offline to 512 Hz and epoched time-locked to the reversal of the annulus (coinciding with the presentation of the disc on trials in which a disc was presented). Epochs were extracted from 250 ms before reversal to 900 ms after, with the mean amplitude of the 100 ms period before reversal subtracted off as baseline. Trials were inspected for eye movement artefacts on the basis of VEOG channels. Trials in which the absolute difference between electrodes placed on the skin above and below the left eye did not remain below 200 μ V for the entire duration of the trial were removed. Artefact-free trials were submitted to further analysis. To avoid introducing any systematic bias in our dataset which might lead to classification performance, no artefact rejection procedures were applied on the basis of the 64 scalp electrodes.

Unfiltered single trials were used to train a linear discriminant classifier using all 64 available electrodes (Carlson, Schrater, & He, 2003). Separate classifiers were trained and tested for each time-point in the EEG epoch. In comparisons where the classifier was trained and tested on the same trial types, the classifier was trained on half of the available dataset and tested on each of the individual trial from the other half. This was repeated, switching the roles of training and test set, such that each individual trial was classified exactly once. In comparisons where the classifier

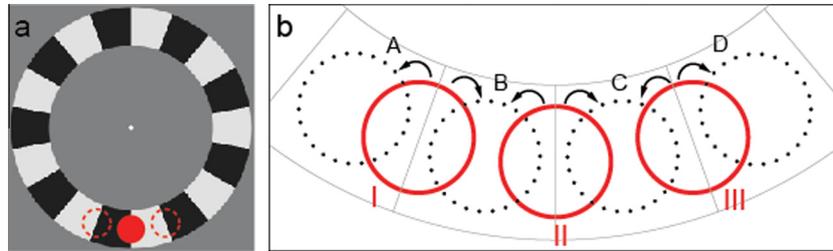


Fig. 1. Stimulus used in the experiment. (a) The stimulus consisted of a rotating annulus that repeatedly reversed direction. At each reversal, a colored disc could be presented at one of three possible locations. (b) Due to the flash grab illusion, the reversal direction of the annulus shifted the perceived location of the disc away from its veridical location. In this way, a disc presented in one of the three veridical locations (I, II, or III) is perceived shifted toward one of four possible perceived locations (A, B, C, or D). Importantly, stimuli presented in veridically identical positions can be perceived in different locations (e.g. I-A vs I-B), and stimuli presented in different positions can be perceived in (approximately) the same location (e.g. I-B and II-B). A [demo video](#) of the stimulus is available (the demo is recorded for display at 60 Hz, so it is less smooth than the version displayed in the actual experiment). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was trained and tested on different trial types, all available data were used for both training and test. In all cases, training and test sets were independent and chance performance was 50%. To calculate 95% confidence intervals of classification performance within each observer, we bootstrapped the classification procedure. Trials in each of the two categories were shuffled 200 times, generating new training and test sets each time. The mean classification performance of the 200 repetitions within each subject was taken as that observer's classification performance. Finally, mean classification performance and the upper and lower limits of 95% confidence intervals were averaged across observers.

3. Results

3.1. Veridical location

Trials were collapsed across reversal directions, and a classifier was trained to discriminate the veridical location of the disc. Separate classifiers were trained and tested for each pairwise combination of the three possible veridical locations (i.e. I vs II, II vs III,

and I vs III; see Fig. 1). Fig. 2 shows the evolution of classification performance over time for each of these comparisons.

Next, separate classifiers were trained to distinguish trials *with* a disc from trials where No Disc was presented. This was done separately for each of the three veridical locations, collapsed across reversal directions (i.e. I vs No Disc, II vs No Disc, and III vs No Disc). Performance over time was averaged across these three comparisons and served as a control to evaluate when any information indicating the presence or absence of a disc is first evident in the EEG signal (plotted as the dotted black line in Fig. 2).

Classification performance was tested against chance at each time-point in two ways. First, we directly compared the lower 95% confidence interval of classification performance (estimated by bootstrapping) to chance (50%). Second, we tested classification performance using a conservative comparison against the binomial distribution with an uncorrected alpha level of 0.01. Because observers differed in the total number of trials available in the final data-set, we adjusted the total number of trials used in calculating the binomial distribution: rather than using the total number of available trials across all observers (>25,000 for each comparison), we compared performance against the product of the number of

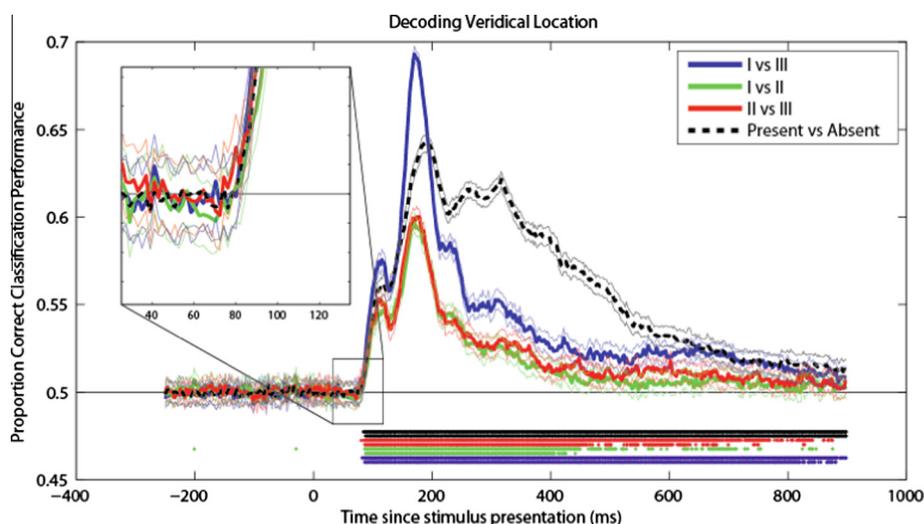


Fig. 2. Performance over time of a classifier trained to discriminate the veridical location of the disc on the basis of EEG activity at individual timepoints. Chance is 50%; above-chance performance at a given time-point indicates that neural activity at that time-point systematically differs between the two types of trials being compared. The black dashed line indicates the average performance of a classifier trained to discriminate the presence or absence of a disc. 95% confidence intervals of each line are plotted as faint lines. The inset shows the initial deviation from chance performance, illustrating that the very first available information indicating the presence of a disc also encodes its location. Significant deviation from chance is indicated by colored dots below the x-axis; for each color, the top row of dots indicates that the bootstrapped 95% confidence interval of classification performance excludes chance level (50%). The bottom row of each color indicates that classification performance is significant at $p < 0.01$ by conservative comparison to a two-tailed binomial distribution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

observers and the minimum number of trials per subject (range 20,000–20,380 for the three comparisons). This adjustment avoided overestimating the contribution of a single observer with a low number of available trials and therefore avoided increasing the chance of Type II error.

Classification performance in the Disc vs No Disc comparison first becomes significantly above chance at 84–88 ms post-stimulus depending on the chosen test and alpha level. Ignoring two spurious timepoints before stimulus onset, classification performance in each of the three pairwise comparisons of disc locations first becomes significant at 80–88 ms post-stimulus. The concurrent rise in classification performance across these comparisons indicates that the very first information available in the EEG indicating the presence of a disc is also informative as to its location. Given the known dependence of early visual ERP components on stimulus position (e.g. Jeffreys & Axford, 1972), and previous work demonstrating that multivariate approaches are able to decode stimulus position from MEG data with comparable accuracy (Carlson et al., 2011), this is an expected result. Nonetheless, it serves to illustrate that the classification approach is able to derive information from the EEG scalp distribution as we might expect.

3.2. Illusory effects of motion on perceived position

We investigated the illusory influence of the flash-grab illusion on the perceived position of the disc in three different ways.

3.2.1. Inwards and outwards illusory shifts

Two separate sets of classifiers were trained to distinguish trials with discs flashed in adjacent veridical positions and opposite reversal directions. The first set was trained to classify the combinations of trials where the flash-grab illusion shifted the perceived locations of the two discs closer together (“Inwards”; i.e. I-B vs II-B and II-C vs III-C). The second set was trained to classify the combinations of trials where the flash-grab illusion shifted the perceived locations of the two discs further apart (“Outwards”; i.e. I-A vs II-C and II-B vs III-D). Note that both sets were trained to discriminate between trials with equal distance between the veridical position of the disc and with opposite reversal directions. The only difference between the two sets of classifiers is how these two factors were combined.

Because in each case the trial types differed in their reversal direction, we also trained a classifier to distinguish between reversal directions on trials where No Disc was presented. This served as a control to show what level of classification performance could be achieved based only on reversal direction.

Fig. 3 shows the performance of the Inwards and Outwards classifiers over time, as well as the No Disc control condition. Classification performance in the Outwards condition exceeds performance in the Inwards condition, indicating that the additional perceptual distance between the two trial types in this comparison is also associated with additional distance in neural representation space. In other words, when the illusion makes the two percepts more different, the associated patterns of neural activity are also more different. Testing whether classification performance between the two classifiers differed by requiring each of the 95% confidence intervals to exclude the mean of the other condition revealed that the Inwards and Outwards condition first significantly differ at 81 ms post-stimulus. Even when using an alternative more conservative approach of requiring that 95% confidence intervals of the two estimates exclude one another entirely, the Inwards and Outwards condition differ significantly at 88 ms. Altogether, it is clear that the two curves start to diverge from the very first moment that they start to deviate from chance, concurrently with the first EEG evidence that a disc is even present. As

such, the earliest EEG signals coding for position are already affected by interactions with motion signals.

3.2.2. Direct comparison of illusory position

To directly compare the perceived position of the disc, a classifier was trained to discriminate the perceived position of the disc separately for each veridical position. In each comparison, discs in the two trial types were therefore in identical veridical positions, but differed in perceived position depending on the reversal direction of the annulus (i.e. I-A vs I-B, II-B vs II-C, and III-C vs III-D). Classifier performance for each of these comparisons over time was collapsed across comparisons. As in the previous analysis (3.2.1), each of these comparisons involved trials with opposite reversal directions, so classification performance on trials without a disc served as a control condition to indicate the performance that could be achieved by decoding only reversal direction (Fig. 4).

As is evident in Fig. 4, classification performance in the Illusion condition exceeds classification performance in the Control condition only for a brief period. When performance in each of the two comparisons is compared by requiring that 95% confidence intervals for each condition exclude the mean of the other condition, the two conditions first statistically differ at 88 ms post-stimulus.

In principle, it is conceivable that the additional decoding performance in the Illusion condition reflects an improvement in the ability of the classifier to decode motion direction due to a non-linear interaction with a direction-irrelevant response to the presentation of the disc (for example caused by visual attention), rather than decoding the disc’s illusory position per se. However, the time-course of the effect corresponds precisely to a comparison of inwards versus outwards illusory shifts (3.2.1) as well as to a cross-classification of illusory position (3.2.3, below). Because these other comparisons cannot be explained by non-linear interactions with direction-irrelevant processes, we believe it is likely that the classifier performance we observe here in the direct comparison of illusory position does in fact reflect an ability to decode the illusory position of the disc. Fig. 6 shows the effects of all three analyses in one figure.

3.2.3. Cross-classification of illusory position

In our final analysis, we trained a classifier to discriminate between trials with discs presented in the two lateral locations, whereby the flash-grab illusion shifted the perceived position of the disc inwards toward the vertical midline (i.e. trial types I-B vs III-C). However, rather than testing the classifier on the same trial-types, we tested the classifier on trials in which the disc was presented in the central location, with the flash-grab illusion shifting the perceived position of the discs away from the vertical midline (i.e. trial-types II-B and II-C). The training and test sets therefore differed in the veridical positions of the discs, but overlapped with regard to the perceived positions of the disc.

Fig. 5 shows the cross-classification performance of this classifier trained and tested on separate trial types. It shows two clear peaks in performance, before converging to an asymptote at the performance which can be ascribed to decoding the reversal direction of the annulus. The implications of the second peak are further studied in Section 3.4, below. Because decoding reversal direction would lead a classifier to label I-B trial as III-C rather than II-B (because they share the same reversal direction), decoding reversal direction leads to below chance performance.

We did not estimate confidence intervals for the cross-classification performance. Because this classifier was trained and tested on separate trial types, it was trained on all available data. As a result, any resampling would reduce the resolution with which the two trial types in the test set might be distinguished and result in lower performance. Instead, we tested whether the two conditions differed by estimating the 99% (rather

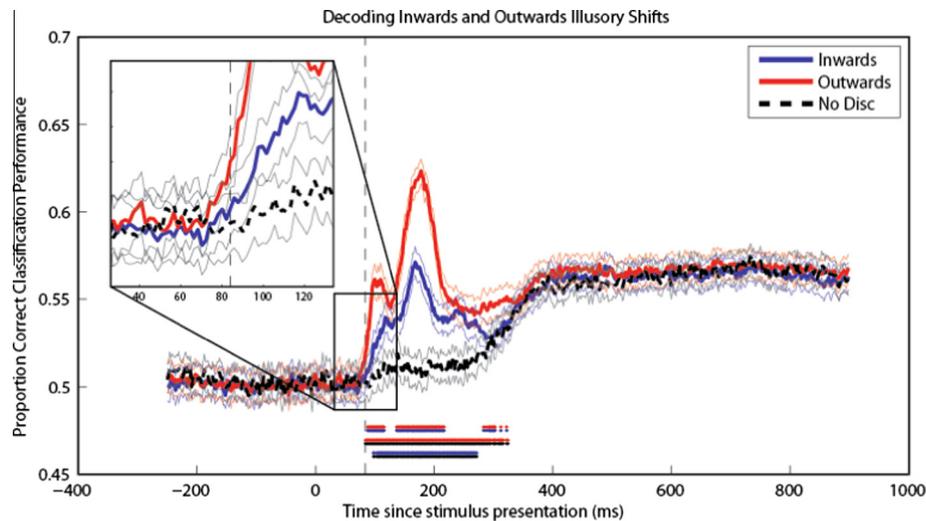


Fig. 3. Classification performance over time of classifiers trained to distinguish trials where the perceived positions shifted closer together due to the illusion (Inwards) and classifiers trained to distinguish trials where the perceived positions shifted further apart (Outwards). The thick black dotted line indicates classification performance in the No-Disc condition, indicating the baseline level of performance that can be expected based on decoding of reversal direction alone. Dotted lines indicate 95% confidence intervals of classification performance in all cases. Rows of paired colored dots below the plotted lines indicate that 95% confidence intervals of the corresponding lines exclude one another at that timepoint, providing a conservative test that classification in one condition outperforms the other at that timepoint. The inset provides an enlarged view of the first deviation from chance, emphasizing the divergence of classification performance in the Inwards and Outwards conditions from the very first moment deviation from chance. The vertical dashed line at 84 ms indicates the first timepoint at which classification of veridical location (see 3.1 in text) was significantly above chance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

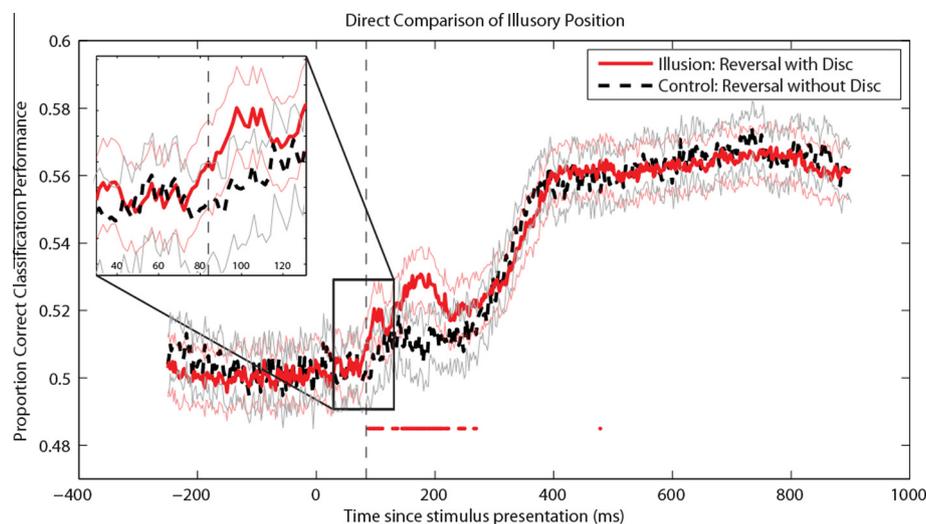


Fig. 4. Classification performance over time of a classifier trained to discriminate reversal direction of the annulus, both for trials with a disc and without. In the Illusion condition, a disc was presented at the reversal, leading to the flash-grab illusion which caused the disc to be perceived in different locations for clockwise and counter-clockwise reversals. In the control condition, No Disc was presented. Because in both cases the two trial types being compared differed in reversal direction, the control condition served as a baseline to indicate the performance that could be achieved by decoding reversal direction alone. 95% confidence intervals are indicated with dotted lines. The vertical dashed line at 84 ms indicates the first timepoint at which classification of veridical location (see 3.1 in text) was significantly above chance. The row of dots below the curves indicates timepoints at which 95% confidence intervals of classification performance in each condition exclude the mean classification performance of the other condition.

than 95%) confidence interval for the control No Disc condition, and assessing whether cross-classification performance fell outside of this range. On the basis of this criterion, cross-classification performance first rose above the performance that can be achieved by decoding reversal direction alone at 88 ms post-stimulus.

As in the direct comparison of illusory position (3.2.2), in this analysis we use No-Disc trials as a baseline for classification performance. This introduces the possibility of non-linear interactions with direction- or position-invariant processes affecting classification performance. However, it is important to note that such interactions can only either amplify a decoding effect or reduce it toward chance. In the present analysis, decoding motion direction

leads to *below*-chance classification assignments to the illusory position, whereas the peaks we observe are *above* chance. As such, these peaks in classification performance cannot be explained by non-linear interactions with direction- or position-invariant processes.

3.3. Localizing illusory effects of motion on perceived position in space and time

Each of the three classification analyses is systematically affected by the ability of the classifier to decode the reversal direction from the stimulus, evident in Figs. 3–5 as asymptotic

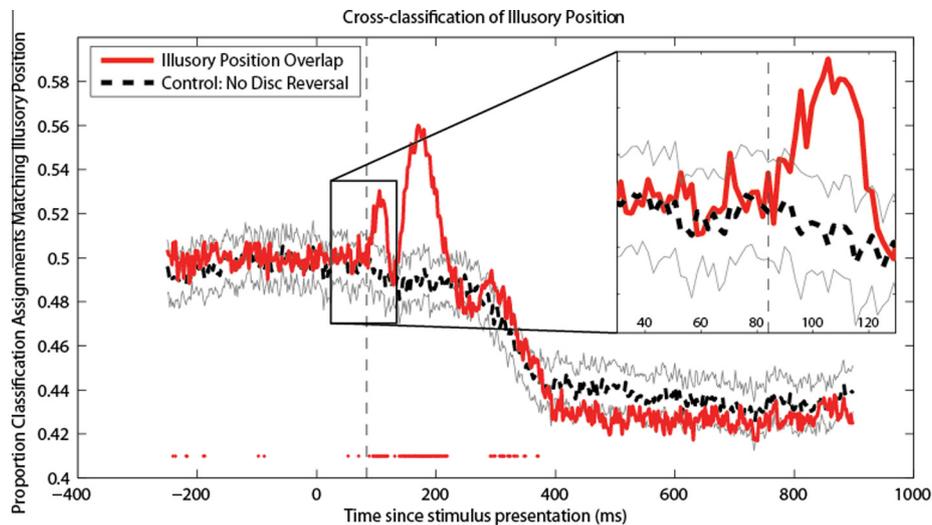


Fig. 5. Cross-classification performance over time of a classifier trained to discriminate trial types I-B and III-C, and tested on trial types II-B and II-C. Although training and test set therefore differed with regard to the veridical location of the disc, the flash-grab illusion caused the perceived positions to overlap between training and test sets. Because in this analysis decoding reversal direction leads to below-chance performance, cross-classification is compared against the inverse of the level of classification performance which can be achieved based on reversal direction decoding alone (black dotted line). 99% confidence intervals for classification performance in the control condition are indicated with dotted lines. The vertical dashed line at 84 ms indicates the first timepoint at which classification of veridical location (see 3.1 in text) was significantly above chance. The inset shows an enlarged view of this period. The row of dots below the curves indicates timepoints at which cross-classification performance falls outside the 99% confidence intervals of the inverse of classification performance in the control No Disc condition.

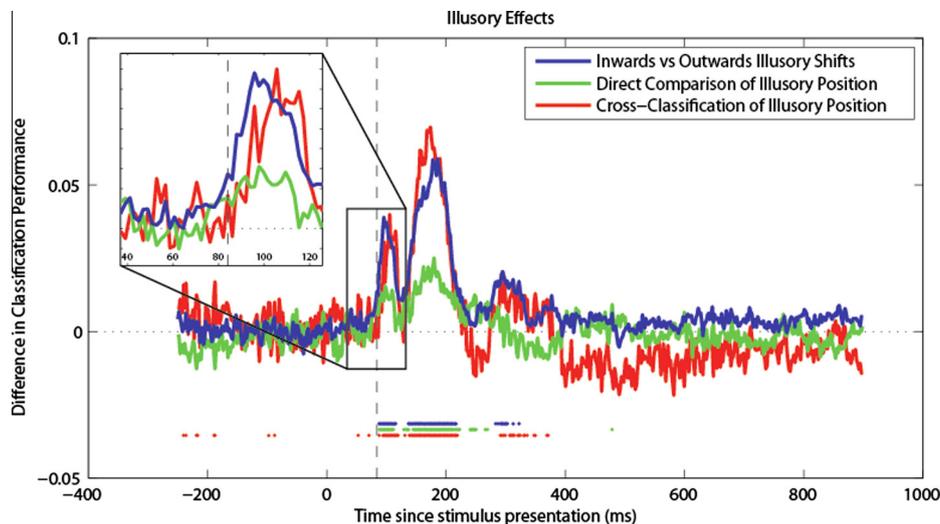


Fig. 6. Corrected Illusory Effects. In each of the three analysis approaches, classification performance is affected by the ability of the classifier to decode the reversal direction of the annulus. This figure combines evidence from all three analysis approaches, each corrected by the respective control condition. The blue line indicates the increase in classifier performance that results from comparing two trials which are perceived to be more different due to the flash-grab illusion, as compared to trials that are perceived to be more similar. The green line indicates the increase in classifier performance that results from presenting a disc at a reversal of the annulus, as compared to decoding reversal direction alone. The red line indicates the increase in cross-classification performance that can be achieved by a classifier trained and tested on trials with different veridical stimulus position, but similar illusory position, as compared to decoding reversal direction alone. The vertical dashed line at 84 ms indicates the first timepoint at which classification of veridical location (see 3.1 in text) was significantly above chance. Each of the three rows of colored dots indicates time-points at which a significant illusion effect was observed (see text for details). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

performance above or below chance. To compare conclusions from each of the analyses, we corrected each comparison by the appropriate control condition. To compare inwards and outwards illusory shifts (3.2.1) we subtracted classification performance on the comparison of inwards trials from classification performance on the comparison of outwards trials. The direct comparison of illusory position (3.2.2) is confounded by reversal direction of the annulus, so we subtracted classification performance when classifying trials in which No Disc was presented from classification performance in which a disc was presented. Finally, the cross-classification of illusory position (3.2.3) is confounded by

reversal direction in the same, but opposite way: classifying trials by reversal direction would lead to below-chance classification performance. Therefore, we subtracted the inverse of classification performance on the comparison of No-Disc trials. The resulting three curves are shown in Fig. 6. Importantly, it is evident from the figure that each comparison demonstrates a comparable time course for illusory position decoding, with the initial rise in classification performance being concurrent with the very first evidence of the disc's presence.

The fact that interactions between visual motion and position signals are evident at the very onset of cortical visual processing

imposes constraints on where these interactions could take place in the visual processing pathway and on the degree to which cortico-cortical feedback could play a role in generating the illusion. Specifically, our results indicate that motion–position interactions are already evident in the first position signal to reach the cortex, restricting possible loci of interaction to those areas that receive visual input from subcortical areas. This naturally includes the primary visual cortex, but also includes area MT and the frontal eye fields (FEF), both of which receive extrageniculate input through the superior colliculus (Lynch, Hoover, & Strick, 1994; Rodman, Gross, & Albright, 1990).

The frontal eye fields are classically seen as being quite far up the visual processing hierarchy (e.g. Felleman & Van Essen, 1991). However, neurons in macaque FEF respond relatively rapidly (e.g. Lamme & Roelfsema, 2002; Schmolesky et al., 1998), and also EEG studies in humans have also shown surprisingly low-latency responses at frontal electrodes (e.g. Kirchner et al., 2009; Thorpe, Fize, & Marlot, 1996), which are thought to arise from this area. Furthermore, based on the characterization of supragranular layer neurons in non-human primates, Barone et al. (2000) noted that projections from FEF to area V4, which is classically seen as earlier in the visual hierarchy, are characteristic of feed-forward, rather than feedback processing. In order to evaluate whether the motion–position interactions we see reflected in our data arise from FEF, we re-ran our three analyses after excluding all central and frontal electrodes (all C, FC, F, Fp and AF electrodes in the international 10–20 system). This left 31 occipital, parietal, and temporal electrodes. Classification performance remained virtually identical in all analyses (Fig. 7, left panel). Next, we reran the analysis on the other half of the available electrodes, thereby excluding all occipital, parietal, and temporal electrodes (Iz and all O, PO, P, CP, and T electrodes). This left 33 frontal and central electrodes. When these electrodes were removed, the patterns of classification performance that corresponded to illusory position shifts were virtually absent (Fig. 7, right panel). The limited spatial resolution of EEG did not allow us to narrow down the source of the neural signal corresponding to the illusory percept even further, for example to discriminate between a source in MT and a source in V1. We also cannot entirely rule out the possibility that FEF might be involved in generating the illusion, but that the relatively small size of FEF

prevents its activity from being detected in the EEG signal until its projections to larger occipital areas become evident at posterior electrodes. Nevertheless, these analyses indicate that measured activity at frontal electrodes does not correspond to the illusory percept, thereby making a role for FEF in the development of the illusory percept less likely and providing more support for a locus of interaction in occipital or parietal cortices.

3.4. Periodic recurrences in classification performance

Each of our three analysis approaches revealed two consecutive peaks of increased neural correspondence to the illusory percept, the first peaking around 100 ms post-stimulus and the second peaking around 180 ms post-stimulus. One possibility is that the first peak reflects feedforward processing as part of the “feedforward sweep”, with the second peak reflecting back-projections to anatomically earlier areas, consolidating the illusory position for subsequent conscious awareness (Lamme & Roelfsema, 2002). However, further analysis of the temporal structure of our data suggests that the two peaks in fact reflect recurrences in the same areas. In fact, the evolution of classification performance over time when decoding real stimulus location suggests a possible third peak (Fig. 2), which also seems to be weakly present in some of our other analyses (Fig. 6). If true, this would imply additional recurrences of the neural patterns corresponding to perception, an observation that is in line with recent reports of perceptual echoes in human occipital cortex (VanRullen & MacDonald, 2012). At the level of individual observers, some observers showed very strong oscillations in classifier performance when classifiers were trained and tested on different time-points (the temporal generalization method; King & Dehaene, 2014). Fig. 8 shows the temporal generalization matrix for a classifier trained to discriminate between veridical locations I and III at each possible combination of training time-point and test time-point. Importantly, the fact that a classifier trained on an early time-point can generalize to a later time-point indicates that the same neural representation becomes reactivated, indicating recurrences in the same area.

VanRullen and MacDonald (2012) report that patterns of neural activity corresponding to a given percept recurred at a rate of 10 Hz – a repetition frequency that roughly matches the timing

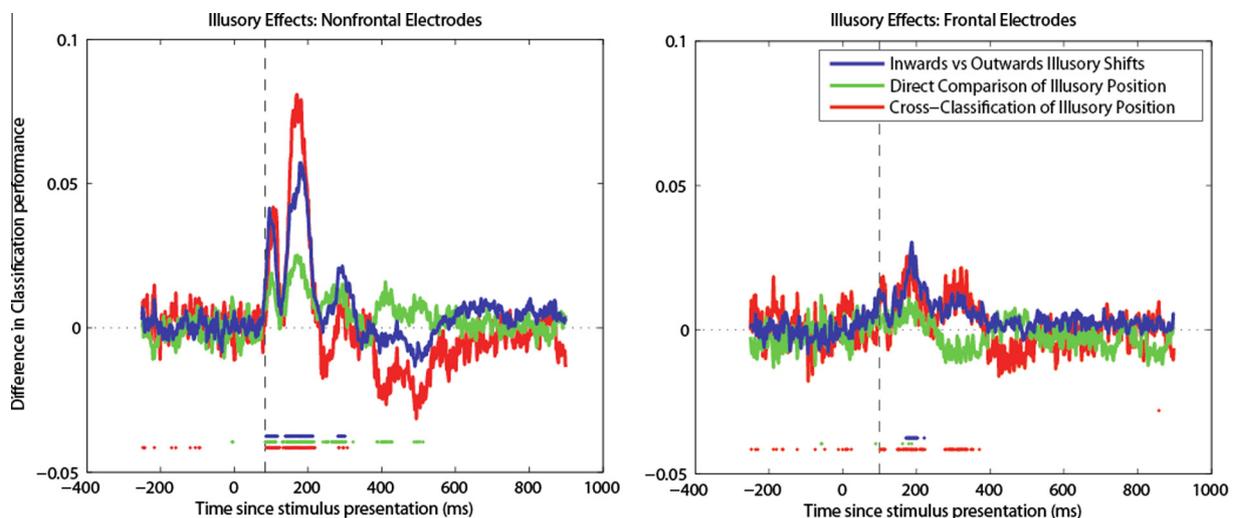


Fig. 7. Corrected Illusory Effects for different electrode subsets. The left panel shows effects for classifiers trained and tested using only temporal and posterior electrodes (CP, P, PO, O, I and T). The right panel shows effects for classifiers trained and tested using only frontal and central electrodes (AF, F, FC, Fp, and C). All other analysis parameters are identical to previous analyses using all available electrodes. Rows of colored dots below each plot indicate time-points at which illusion effects are significant (see text of corresponding analysis for details). The effects evident in Fig. 7 are clearly driven by patterns of activity over the posterior scalp (left panel), with the illusory effects virtually absent when these electrodes are excluded from the analysis (right panel). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

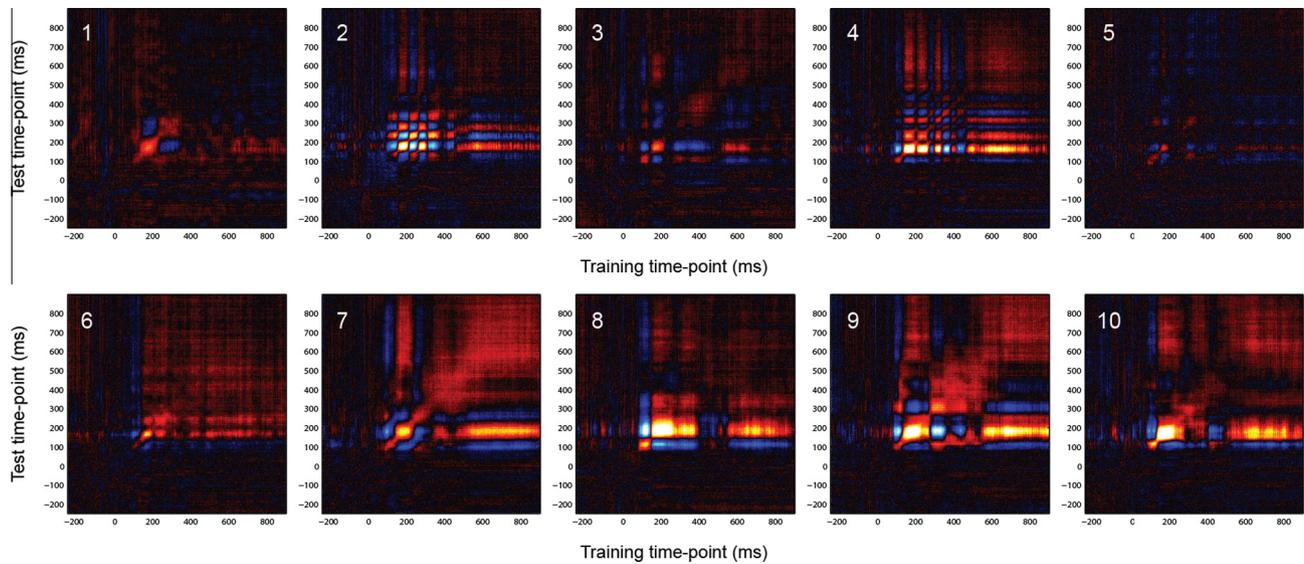


Fig. 8. Temporal generalization matrices for each of the ten individual observers, for a classifier trained to discriminate veridical locations I and III. The classifier is separately trained and tested at each combination of timepoints. The *x*-axis shows training timepoint, and the *y*-axis shows test timepoint, with warm colors indicating above-chance performance and cool colors indicating below chance performance. Each panel represents an individual observer. Several observers shows a clear recurrence of earlier neural representations, as evidenced by alternating hot and cool patches. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

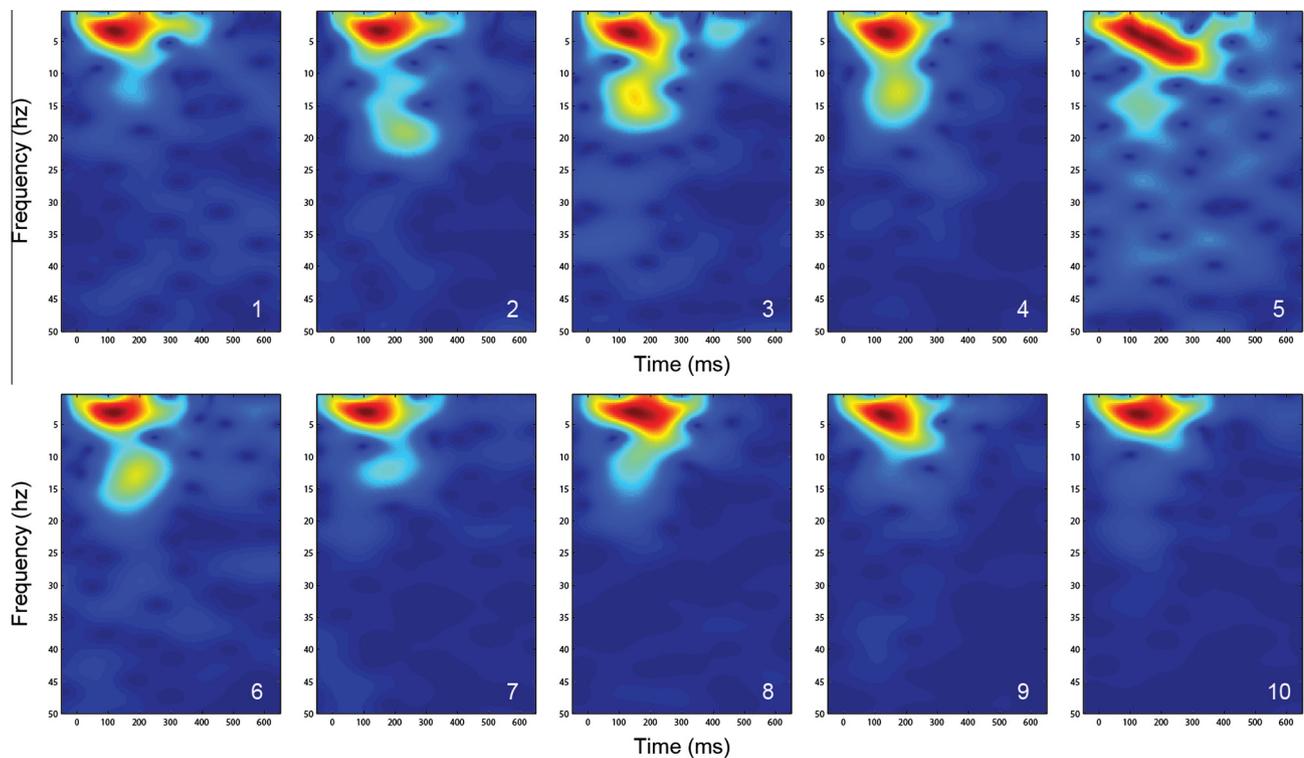


Fig. 9. Time-frequency decomposition of classification performance in each of the ten individual observers. The classifier was trained to discriminate between veridical locations I and III, at corresponding training and test time-points. In addition to the main blob of spectral power reflecting the main rise and fall of classification performance, a number of observers demonstrate oscillations in performance at higher frequencies (~ 10 – 20 Hz).

between consecutive peaks in some observers in our data. Fig. 9 shows a time-frequency analysis of classification performance at corresponding training and test time-points (i.e. the diagonal of each of these generalization matrices, which is equivalent to the blue line in Fig. 2). These “perceptual echoes” (VanRullen & MacDonald, 2012) recurred more strongly in some observers than others, and at slightly different frequencies.

4. Discussion

A variant of the flash-grab illusion (Fig. 1a and b; Cavanagh & Anstis, 2013) was used to shift the perceived location of flashed objects. We applied multivariate pattern classification to single-trial EEG data, acquired while observers were viewing this illusion, to dissociate neural signals corresponding to veridical as

opposed to perceived position. This allowed us to separate patterns of neural activity corresponding either to sensory input or perceptual interpretation with high temporal resolution. In three different lines of evidence, we show that neural correlates of motion-induced position shifts in perception are evident as early as 84 ms post-stimulus, concurrent with the very first stimulus-related activity that could be recorded from the scalp:

- (1) A classifier is better able to discriminate two trials when the flash-grab illusion pushes the perceived positions of the discs apart, than when it pushes the perceived positions of the discs closer together. In other words, the more similar the perceived positions of the two discs, the more similar the corresponding neural representations and the harder it becomes for the classifier to discriminate between them (even when the distance between the *actual* positions of the two discs remained identical).
- (2) A classifier trained to distinguish trials with different reversal directions performs better when a disc is presented in identical veridical positions (but shifted to different perceived positions due to the illusion) than when No Disc is presented at the reversal.
- (3) Finally, a classifier trained to discriminate trials in which the stimulus is presented in the central location (II), but successively tested on trials in which the stimulus was presented in the outer location (I and III), performs above chance when the *perceived* (but not veridical) positions of the discs in the training and test set are close together.

All three analysis approaches reveal significant illusion effects on the very first cortical activation, within 88 ms following stimulus presentation. The strikingly low latency of the start of motion–position interactions indicates that these interactions already occur (or have occurred) immediately upon entering the cerebral cortex, without requiring cortico-cortical feedback connections. This severely constrains the possible brain areas that might underlie these interactions. Applying our classification analysis to smaller subsets of electrodes suggests that one possible candidate, the frontal eye fields, are unlikely to be the initial locus of interaction, leaving areas in occipital and parietal cortices as more likely candidates. But which cortical areas receive motion input rapidly enough to calculate motion–position interactions *concurrently* with the development of retinotopic position representations in primary visual cortex?

One possibility is that motion–position interactions occur in V1 itself. However, although motion-dependent effects on V1 position-coding have been demonstrated, the effects tend to be substantially smaller than perceptual effects (e.g. Fu et al., 2004; Kosovicheva et al., 2012) or even in the opposite direction (Whitney et al., 2003). Kosovicheva et al. (2012) reported shift magnitudes putatively localized to V1 of about 10% of the perceptual magnitude. Similarly, Cavanagh and Anstis (2013) showed that when attention is made unavailable, the flash-grab effect is reduced to roughly 10% of its initial magnitude. Although there does therefore seem to be a small effect of motion on position tuning in V1, thalamo-cortical activation of V1 does not seem to be the neural basis for motion–position interactions *in perception*. Instead, V1 motion–position interactions might reflect back-projections from extrastriate areas (for example MT) to V1. Sundberg, Fallah, and Reynolds (2006) showed that although retinotopy in monkey V4 could be shifted by concurrent motion, these effects could be dissociated from motion–position interactions in perception, suggesting that some such effects in early visual cortex might be epiphenomenal. This interpretation is also consistent with previous reports that rapid projections from MT to V1 are necessary for the conscious perception of moving phosphenes induced by

TMS (Pascual-Leone & Walsh, 2001). It therefore seems likely that motion–position effects in V1 might result from projections from other areas to V1 – but carrying signals that arrived in those areas independently, through rapid extra-geniculate pathways, rather than as re-entrant feedback processes first originating and then returning to V1.

The two cortical areas most strongly implicated in previous research into motion-induced position shifts in humans are areas V3A and MT. For example, Maus et al. (2010) found predictive activity in area V3A, with stronger fMRI responses for motion toward versus away from a given voxel's ROI. Disrupting MT activity with TMS reduces the flash-lag effect (Maus, Ward, et al., 2013; McGraw, Walsh, & Barrett, 2004), and both MT and V3A show patterns of neural activity that correspond to the illusory position of an object whose perceived position is shifted by the flash-drag effect, as opposed to its veridical position (Maus, Fischer, & Whitney, 2013).

Although V3A and MT are both classically seen as anatomically midlevel areas (Felleman & Van Essen, 1991), anatomical descriptions of the visual processing hierarchy do not necessarily correspond to temporal descriptions (Lamme & Roelfsema, 2002). Due amongst others to the different speeds of parvocellular and magnocellular pathways, and to extra-geniculate input to the cortex through the superior colliculus and pulvinar, cells in anatomically 'later' areas might actually respond faster than other cells in anatomically earlier areas. In fact, in a review of response latencies of different visual areas in non-human primates, the four visual areas with the lowest mean response latency are V1 (72 ms), V3 (76 ms), MST (74 ms), and MT (77 ms; Lamme & Roelfsema, 2002). Accordingly, the authors propose that the first wave of feedforward activity in response to a stimulus (the "feedforward sweep") actually originates concurrently in V1 and MT, rapidly recruiting V3 before propagating further along the pathway. In this light, our finding of low-latency neural effects corresponding to motion-induced position shifts is actually consistent with previous findings. Given the classical role of MT as a motion area, the known extra-geniculate input to MT (Rodman, Gross, & Albright, 1990), and the fact that TMS over MT (but not V3) impairs the perception of motion in the blind field of blindsight patients (Alexander & Cowey, 2009), area MT seems more likely than V3 or V1 to be the source of the initial interaction.

Finally, it remains possible that motion–position interactions take place in subcortical, rather than cortical brain areas. In particular the superior colliculi (SC) are known to have a number of properties that make them plausible candidates for the neural locus of the present effects. SC receives direct input from the retina, at comparable or even lower latency than the earliest cortical areas (e.g. Bell et al., 2006). Neurons in SC form a retinotopically organized map used in saccade targeting, and have been shown to extrapolate the future position of moving objects as function of their velocity (Fleuriet & Goffart, 2012). Accordingly, some degree of motion–position interaction clearly does occur in this structure. However, it is difficult to say whether extrapolation processes in SC reflect computations based solely on afferent retinal input, or instead rely on back-projections from cortical areas such as the FEF. Due to the distance from the scalp, our EEG observations cannot directly reflect SC activity. Nevertheless, it remains possible that the motion–position interactions that we putatively localize to rapidly-responding visual areas might actually reflect calculations in the superior colliculi. Altogether, our results show that motion-induced position shifts begin very early in visual processing, but not necessarily in anatomically early areas. Taken together with previous literature, our results are most consistent with an early role for area MT as part of a predominantly feed-forward wave of activity.

Although the neural mechanisms underlying the shift in perceived position of the flashed object begin at the very onset of

cortical processing of that object, the time-course of the build-up of the illusion remains unclear. In our data, the direction of the illusory effect on perceived position is evident in the very first cortical signals, but it is difficult to establish whether the magnitude of the shift in neural representation is already comparable to the magnitude of the perceived shift so early. The fact that reducing the availability of attention diminishes the size of the perceptual effect (Cavanagh & Anstis, 2013) suggests that the early neural signal might later be amplified by higher-order processes. In some sense, it seems impossible for the initial rapid neural response to code the final perceived position of the shifted object, because it is the motion after the reversal event that determines the direction and magnitude of the position shift: if the motion is terminated concurrently with the flashed object, the illusion disappears (previously noted by Eagleman & Sejnowski, 2007; see also Cavanagh & Anstis, 2013; Fig. 15). In fact, both Eagleman and Sejnowski (2007) and Cavanagh and Anstis (2013) report that following a flashed stimulus, on the order of 80–100 ms of subsequent motion can contribute to its mislocalization. However, in our results, the direction of the object's illusory shift is already evident in the pattern of cortical neural activity by this time. Logically then, the initial neural response cannot fully represent the final perceived location without violating causality. The mechanism underlying the time-course of this paradoxical, seemingly retroactive mechanism will need further investigation.

5. Conflict of interest

The authors declare no competing financial interests.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2015.05.005>.

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