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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.

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 μV 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