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Report

Misbinding of Color and Motion in Human Visual Cortex

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Summary

A fundamental challenge for the visual system is to integrate visual features into a coherent scene, known as the binding problem. The neural mechanisms of feature binding are hard to identify because of difficulties in separating active feature binding from feature co-occurrence. In previous studies on feature binding [1–5], visual features were superimposed and presented simultaneously. Neurons throughout the visual cortex are known to code multiple features [6]. Therefore, the observed binding effects could be due to the physical co-occurrence of features and the sensory representation of feature pairings. It is uncertain whether the mechanisms responsible for perceptual binding were actually recruited [7, 8]. To address this issue, we performed psychophysical and fMRI experiments to investigate the neural mechanisms of a steady-state misbinding of color and motion [9], because feature misbinding is probably the most striking evidence for the active existence of the binding mechanisms [10]. We found that adapting to the color-motion misbinding generated the color-contingent motion aftereffect, as well as the color-contingent motion adaptation effect in visual cortex. Notably, V2 exhibited the strongest adaptation effect, which significantly correlated with the aftereffect across subjects. Furthermore, effective connectivity analysis using dynamic causal modeling showed that the misbinding was closely associated with enhanced feedback from V4 and V5 to V2. These findings provide strong evidence for active feature binding in early visual cortex and suggest a critical role of reentrant connections from specialized intermediate areas to early visual cortex in this process.

Results

We used a modified version of the steady-state misbinding illusion reported by Wu and colleagues [9]. Our stimuli (Figure 1A) contained two sheets of isoluminant dots, one sheet moving up and the other moving down. On both sheets, dots in the right peripheral area (right of the white dashed line, effect part) and those in the rest area (induction part) were rendered in different colors (red or green). Intriguingly, when observers fixated at the center of the stimulus, during most of the viewing time, the color and motion of the dots in the effect part were perceived to be bound in the same fashion as those in the induction part. For example, for the left stimulus in Figure 1A, on the upward-moving sheet, dots in the induction and effect parts were red and green, respectively. On the downward-moving sheet, dots in the induction and effect parts were green and red, respectively. The misbinding of color and motion made observers perceive upward-moving red dots and downward-moving green dots in the effect part.

Psychophysical Experiments

In the psychophysical adaptation experiment, we used an aftereffect to investigate whether the human visual system could represent the color-motion misbinding. Adaptation is a general property of almost all neural systems. Due to its power to isolate and temporarily reduce the contribution of specific neural populations, measuring the adaptation aftereffects has been a powerful tool of psychophysics to study the representation of various visual patterns [11]. By using a method of constant stimuli, we measured the color-contingent motion aftereffect (CCMAE) from adapting to the color-motion conjunctions (misbinding or correct binding?) in the effect part. The CCMAE directions predicted from adapting to the misbinding or the correct binding are opposite. From the measured CCMAE direction, we can infer whether the misbinding or the correct binding is represented in visual cortex. The experiment was composed of two adaptation conditions. In the first condition, adaptors contained both the induction and effect parts (Figure 1A). In the second condition, adaptors contained only the induction part (Figure 1B). Test stimuli were red or green dots presented in the effect part, moving with one of five speeds (0.6°/sec upward, 0.3°/sec upward, 0°/sec, 0.3°/sec downward, 0.6°/sec downward). After 30 s preadaptation and 5 s topping-up adaptation, a test stimulus was presented for 0.2 s, and subjects made a two-alternative forced-choice (2-AFC) judgment on the motion direction of the test stimulus, either upward or downward.

Because data from the red and green test stimuli showed as a similar pattern, they were pooled together for analysis. Unless otherwise stated, we present average data across 12 subjects hereafter. Figure 2A shows the psychometric functions for the two adaptation conditions. We plotted the percentage of trials in which subjects indicated directions for the test stimuli that were opposite to the perceived direction of adapting dots (which possessed the same color as the test stimuli) as a function of the real speed of the test stimulus. After subjects adapted to the induction part only (the second condition), they gave nearly perfect performances for all the test stimuli (about 50% level for the 0°/sec stimulus, good judgment for the 0.3°/sec and 0.6°/sec stimuli). However, after adaptation to the induction and effect parts (the first condition), the psychometric function showed a horizontal left shift. In other words, subjects' perception of the moving direction of the test stimuli was biased opposite to the perceived (rather than the physical) moving direction of the adapting dots (with the same color as the test stimulus), suggesting that subjects' visual cortex adapted to the misbinding. To quantitatively measure the CCMAE magnitude, we fit the psychometric

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values at the five test speeds with a cumulative normal function for each adaptation condition. We interpolated the data to find the speed expected to be perceived stationary. The speed difference between the two conditions (mean ± SEM: 0.1229 ± 0.0123) was the CCMAE from adapting to the effect part, which was significantly above zero ($t_{11} = 9.996$, $p < 0.001$, Figure 2B).

In a separate experiment, we measured the percentage of time that subjects perceived the color-motion misbinding when they viewed the stimuli in the first adaptation condition. During preadaptation and topping-up adaptation, subjects pressed one of two buttons to indicate their perceptual state—correct binding or misbinding. They perceived the misbinding on average 80% of the time. Remarkably, the percentage of time was significantly correlated with the CCMAE magnitude across subjects ($r = 0.685$, $p = 0.014$, Figure 2C). Taken together, these results showed that the misbinding determined the CCMAE direction and magnitude, suggesting that neurons in visual cortex encode the color-motion misbinding for the dots in the effect part.

fMRI Experiments

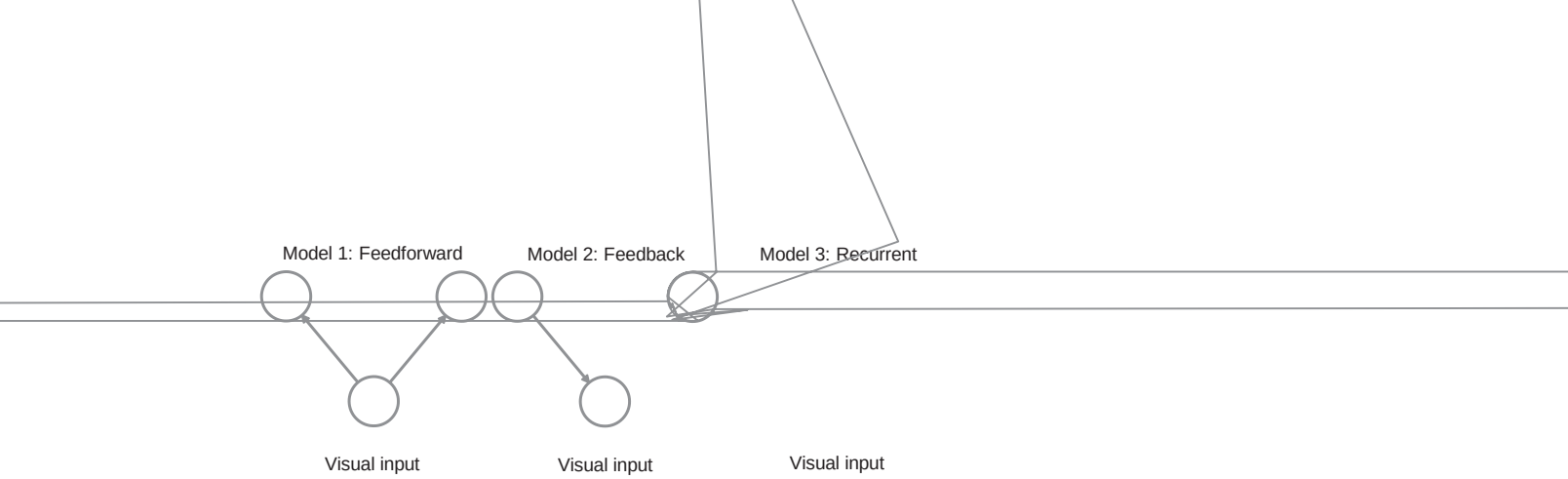
To directly investigate where the misbinding is represented in the brain, an event-related fMRI adaptation experiment was designed to measure the color-contingent motion adaptation effect in cortex. Similar to the psychophysical adaptation experiment, subjects adapted to either the induction and effect parts (first condition) or the induction part only (second condition). After 30 s preadaptation and 5 s topping-up adaptation, a test stimulus was presented for 0.5 s (Figure 1C). There were two test stimuli, each containing both red and green moving dots. In one test stimulus, the dots were identical to those in the effect part of the adaptor (i.e., same trials), whereas dots in the other test stimulus moved in opposite directions to those in the effect part of the adaptor (i.e., opposite trials). For attentional control, subjects needed to press one of two buttons to indicate a 0.2 s luminance change (increase or decrease) of the test stimuli. The luminance changes were determined by adaptive staircases before scanning to ensure that subjects performed equally well for the same and opposite trials.

Regions of interest (ROIs) in V1, V2, V3, V3A/B, V4, V5, and PPC (posterior parietal cortex) were defined as the cortical regions responding significantly to the effect part. Blood-

two conditions are shown in Figure 3C, which reflects the
rotation effect to the effect part. The differences
re in V1–V5 (all $t_{11} > 4.617$, $p <$
566). These results

two parts were combined
same way. In the misbinding condition, they were


% signal change



combined in opposite ways, which was the same as that in the psychophysical adaptation experiment.

The DCM analysis focused on directional connectivities between V2 and V4 and between V2 and V5 based on BOLD signals from these areas. V4 and V5 were selected because they are functionally specialized areas for processing color and motion, respectively. DCMs have three sets of parameters: (1) extrinsic input into one or more regions, (2) intrinsic connectivities among the modeled regions, and (3) bilinear parameters encoding the modulations of the specified intrinsic connections by experimental manipulations [16]. Given the extrinsic input into V2, we defined feedforward, feedback, and recurrent models between V2 and V4 and between V2 and V5 (Figure 4A). The intrinsic connectivity patterns in the DCMs were modeled and then compared by computing the exceedance probability of each model. The result showed that the feedforward, feedback, and recurrent models had exceedance probabilities of 40.71%, 6.70%, and 52.59%, respectively, suggesting that the recurrent model best explains the overall data (Figure 4B).

We next examined modulatory connections in the recurrent model. In DCM, modulatory connections reflect increases or decreases in connectivity between two regions given some experimental manipulation, compared with the intrinsic connections between the same regions that capture connectivity in the absence of experimental manipulation [16]. Figure 4C shows the modulatory connectivities in the three conditions. The effect part condition and the correct binding condition evidenced a similar pattern. The correct binding condition increased the forward connectivities from V2 to V4 (t_{11} = 3.408, p = 0.006) and from V2 to V5 (t_{11} = 8.653, p < 0.001) and decreased the backward connectivity from V5 to V2 (t_{11} = 4.569, p = 0.001). The effect part condition also increased the forward connectivities from V2 to V4 (t_{11} = 5.937, p < 0.001) and from V2 to V5 (t_{11} = 8.653, p < 0.001). However, the misbinding condition showed an opposite pattern: it decreased

the forward connectivities from V2 to V4 (t_{11} = 7.358, $p < 0.001$) and from V2 to V5 (t_{11} = 4.512, $p = 0.001$), but increased the backward connectivities from V4 to V2 (t_{11} = 4.323, $p = 0.001$) and from V5 to V2 (t_{11} = 4.190, $p = 0.002$).

To further evaluate the role of these forward and backward connectivities in the color-motion misbinding, we calculated the correlation coefficients between the CCMAE and the effective connection strengths (the sum of the modulatory and intrinsic connectivities) across subjects (Figures 4D and 4E). The CCMAE was positively correlated with the backward connectivities from V4 to V2 ($r = 0.763$, $p = 0.004$) and from V5 to V2 ($r = 0.602$, $p = 0.038$), but its correlations with the forward connectivities were negative and only marginally significant (from V2 to V4: $r = -0.501$, $p = 0.097$; from V2 to V5: $r = -0.549$, $p = 0.064$). Taken together, the DCM results suggest that the effective connectivities between V2 and both V4 and V5 (especially the enhanced feedback) might significantly contribute to the misbinding.

Discussion

Our study provides the following psychophysical and neuroimaging findings. First, adapting to the color-motion misbinding generated a CCMAE, the magnitude of which was determined by the strength of the misbinding experienced by individual subjects. Second, the visual cortex, but not the PPC, exhibited the color-contingent motion adaptation effect

more common in the superficial and deep layers (1, 2, 5, and 6), which receive feedback connections from V4 and V5, compared with the middle layers (3 and 4), which relay ascending signals. This finding suggests that, relative to feedback pathways, color and motion processing in V2 are more independent in feedforward pathways. Color and motion bound initially in the feedforward pathways could be reintegrated in the feedback layers. Taking into account the neurophysiological findings and our fMRI findings, we might speculate the neural implementation of the misbinding as follows. When subjects view the stimulus in the feedforward pathways, visual information in the induction and effect parts is processed independently. Colors and motion directions are initially bound according to the physical property of the stimulus. When these ascending color and motion signals reach V4 and V5, color-defined surfaces and motion-defined surfaces across the induction and effect parts form in these two areas, respectively [25–27]. Note that the unitary surfaces are not consistent with the physical binding of colors and motion directions in the effect part area. To solve this problem, the surface information guides feedbacks to the superficial and deep layers of V2 and activates neurons that are responsive to the effect part area and are also selective for the color-motion conjunction in the induction part. The V2 reactivation leads to the misbinding illusion. This feedback process is implied by the increased backward connectivities from V4 and V5 to V2, as revealed by the DCM analysis. The decreased forward connectivities in the opposite directions are sensible because the veridical perception reflected by the forward connections has been replaced by the misbinding illusion. It should be noted that our speculation only provides a possible mechanism for the color-motion misbinding, which should be tested with neurophysiological techniques in the future.

In sum, our study provides strong evidence for active feature binding in early visual cortex and implies a critical role of reentrant processing in this process [12]. In the future, various misbinding conditions should be investigated to fully understand the solution of the binding problem, which might also be the solution to the mystery of consciousness.

Supplemental Information

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.04.045.

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