

Neural mechanisms of feature binding

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absence of attention (e.g., [Seymour et al., 2009](#), [Holcombe and Cavanagh, 2001](#)). For example, a psychophysical study showed that spatially superimposed feature pairs could be bound even at an extremely high flickering rate ([Holcombe and Cavanagh, 2001](#)). Adapting to a particular conjunction of features could generate visual contingent aftereffects and these aftereffects occurred specifically for the adapted eye, suggesting that feature binding might occur at the early stage with retinotopic organization. Besides psychophysical studies, some neuroimaging studies also suggest that feature binding takes place in early visual cortex (e.g., [Seymour et al., 2009](#)).

Late binding theories argue that features are bound at a late processing stage and that the parietal cortex is critical for feature binding. For example, patients with lesions in the bilateral posterior parietal cortex (PPC) could perceive illusory feature conjunctions which were not presented ([Braet and Humphreys, 2009](#)). With 1 Hz rapid TMS applied to the right intraparietal sulcus (IPS), participants could make fewer binding errors ([Esterman and Verstynen, 2007](#)). An fMRI study showed that the right temporoparietal junction (TPJ) was also important for the binding of color and spatial frequency ([Pollmann et al., 2014](#)). These findings suggest that the parietal cortex plays a critical role in the binding process.

Feature integration theory and reentrant processes. Feature integration theory (FIT) is a prominent theory providing a general framework of feature binding ([Treisman, 1996](#)). It is worth noting that FIT proposes that attention-dependent reentrant processes are essential for feature binding, which is different with early/late binding theories. According to FIT, visual inputs first activate low-level feature detectors. Feature detectors then communicate to object processing modules in higher cortical areas for generating feature conjunctions. To validate those feature conjunctions, the visual processing stream also needs to trace back to early visual cortex to ensure that visual features are encoded accurately. The critical role of reentrant processing in feature binding is supported by behavioral and neuroimaging studies. [Bouvier and Treisman \(2010\)](#) used the backward masking paradigm to inhibit feedback connections during color-orientation binding and found that subjects made more binding errors. [Koivisto and Silvanto \(2012\)](#) used the same stimuli and applied TMS at different time points after stimulus presentation to interfere with the binding process. Two critical time windows for feature binding were detected: 90 ms for feature detection, and 150 ms for feature binding. When TMS was applied over the angular gyrus to inhibit feedback connections during the latter time window, subjects could not finish the discrimination task, which required correct feature binding.

As we mentioned above, feature misbinding is a powerful tool to verify FIT. [Zhang et al. \(2014\)](#) used psychophysical

and fMRI approaches to explore the cortical mechanisms of feature binding with a color-motion misbinding stimulus. The color-motion misbinding stimulus usually contained two sheets of moving dots: one with upward movement and one with downward movement. On each moving sheet, dots in the central and peripheral areas combine color and motion in opposite fashions. When fixating on the center of the display, observers erroneously perceive the dots in the periphery

pants were required to report their perception (either active binding (misbinding) or physical binding) when the stimulus was presenting. They found that decreased alpha activity was correlated with a higher time proportion of the active binding, and applying tACS at individual alpha-frequency could causally determine the way of color-motion binding, suggesting that more active representations were required for the active binding than for the physical binding. This is in agreement with previous neuroimaging studies, which found that feedback connections were recruited for the active binding (e.g., [Zhang et al., 2014](#)). In addition, individual alpha-frequency was positively correlated with the perceptual switch rate between the two binding states, and applying tACS at different frequencies within the alpha band could causally change