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patients' laughter and mirth occurred using high-frequency ES lasting up to 5 s but not during single-pulse stimulation. Given that ES can have complex and widespread effects in large areas of the brain that are not fully understood [11], the prolonged, high-frequency stimulation may have activated distant cortical or subcortical motor areas.

In conclusion, Gallese and Caruana's concerns seem to arise from the form of our model (arrows and boxes appearing to suggest serial and separate processes) rather than any substantive points of disagreement. However, we further contend that the studies cited by Gallese and Caruana do not in their specifics contradict our initial claims.

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Spotlight

Remapping Attention Pointers: Linking Physiology and Behavior

Martin Rolfs[1,3,*] and Martin Szinte[2,3]

Our eyes rapidly scan visual scenes, displacing the projection on the retina with every move. Yet these frequent retinal image shifts do not appear to hamper vision. Two recent physiological studies shed new light on the role of attention in visual processing across saccadic eye movements.

Saccades are the body's most frequent voluntary movements, yet the constant displacements of the retinal image that they entail appear to be no burden to visual processing. We easily keep track of where things are in the world, despite the fact that the same position in space is processed by a new set of neural populations after each saccade. How do we achieve this visual stability as our eyes are jumping about?

A possible answer began with the finding of predictive remapping of neural activity in so-called priority maps – areas that control spatial attention – including the lateral intraparietal area (LIP), the frontal eye fields (FEF), and the superior colliculus (SC) [1]. Like most visual brain areas, these areas are retinotopic with their neurons responding to stimuli at a particular location on the retina: their receptive field (RF). Remarkably, these areas remap activity prior to saccades: their neurons start responding to stimuli that will land in their RF after the eye movement. Using an efference copy of the motor command, they appear to anticipate the future.

Inspired by these physiological findings, one group of researchers [2] proposed that the attentional system is in an ideal position to orchestrate visual stability. In particular, they argued that the visual system predicts the retinotopic consequences of the next saccade by updating attention pointers – top-down connections from priority maps (e.g., LIP, FEF, and SC) to feature maps (V1–V4, MT), guiding spatial attention (Figure 1). Just before each saccade, attention would be remapped to those retinotopic locations that would soon host the relevant parts of the scene. This account hypothesized two key functional consequences of neural remapping in human behavior: the updating of attention in the opposite direction of the saccade and the facilitation of visual processing at the attended location just after the saccade. Indeed, a series of studies found strong support for a remapping of attention [3–5] and supported its role in providing continuity of perception [4].

However, another group [6,7] recently challenged 'remapping' as a viable mechanism for visual stability. They showed that FEF neurons become more sensitive to stimuli presented in the vicinity of the saccade goal rather than at their remapped locations. Pre-saccadic neural population responses in FEF therefore reflect saccade preparation rather than a trans-saccadic updating of a spatial map as described in neuroscience textbooks. This also raised questions about the nature, origin, and function of remapping of attention [3–5]. Indeed, linking neural evidence of remapping to attention requires tests that go beyond all previous efforts. Two new studies now provide several of these critical tests.

In the first study, Neupane and colleagues [8] mapped out the RF of neurons in area V4, an area selective for features such as orientation, shape, and color that integrates signals from priority maps. They recorded visual responses to the presentation of flashed stimuli at different times before and after saccade. For stimuli presented just

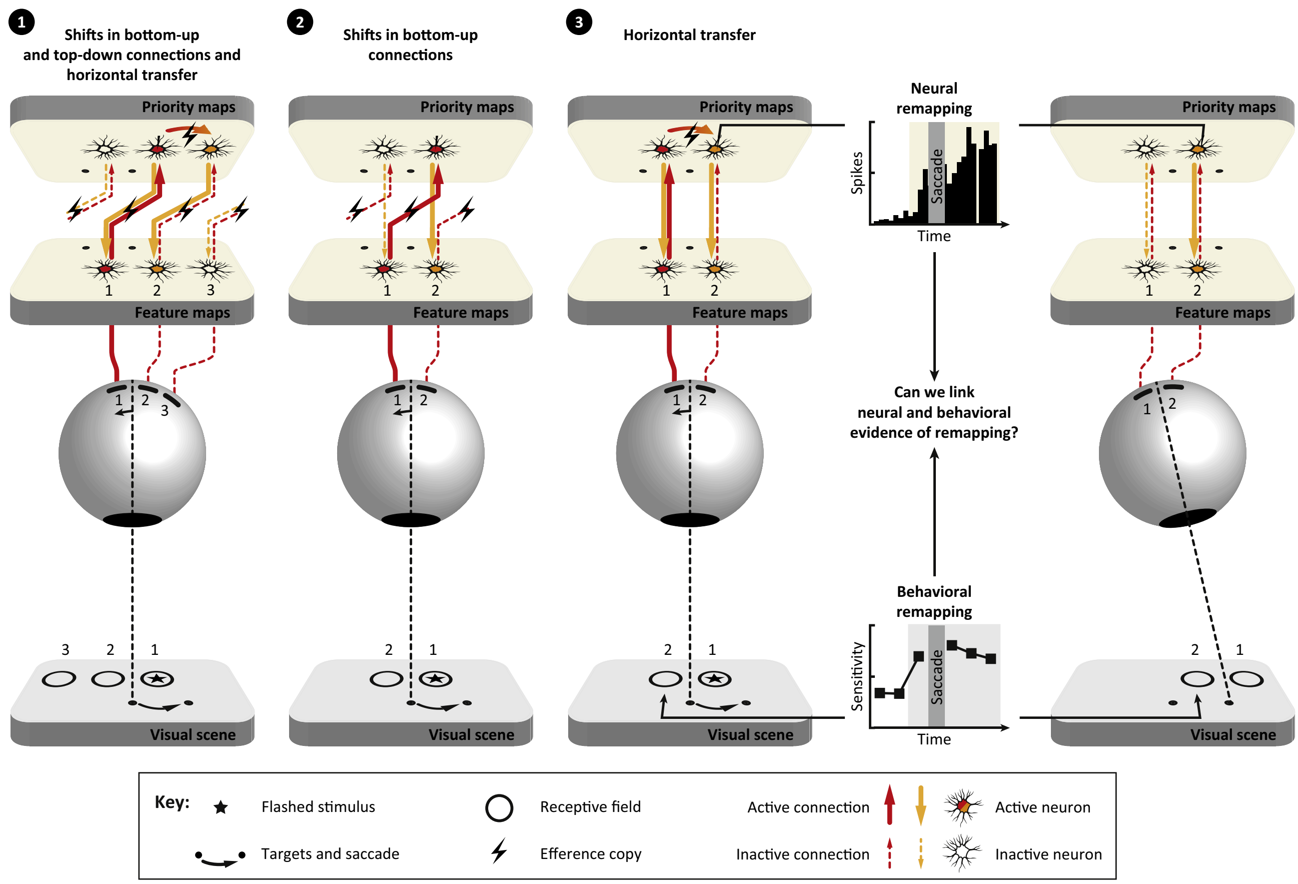

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Figure 1. Three Pre-saccadic Mechanisms Linking Neural and Behavioral Evidence of Remapping. A stimulus flashed in between the fixation and saccade targets (see visual scene) is projected onto the retina, triggering a cascade of bottom-up (red arrows) and top-down (orange arrows) connections throughout the visual processing hierarchy. Each retinal location connects to a specific neuron (in fact, a population of neurons) in retinotopic feature maps (V1–V4, MT). Feature map neurons, in turn, are linked to priority maps (FEF, LIP, SC). Numbers label specific locations on the retina, neurons, and the locations of the RFs of neurons in space. Data panels show neural (top) and behavioral (bottom) evidence of remapping, recorded before the saccade (left panels) from neuron #2 and location #2, respectively. Models predicting both neural and behavioral remapping differ in complexity, but consistently propose that efference copy signals alter the state of top-down or bottom-up connections between priority and feature maps. (1) Just before a saccade, top-down and bottom-up connections shift, linking the post-saccadic location in the priority map to the pre-saccadic location in the feature map. As top-down connections are now offset, behavioral evidence of remapping requires a concurrent horizontal transfer of activity in the priority map [10]. (2) Only bottom-up connections shift (generating neural remapping), whereas the unaltered top-down connections result in remapping of attention. These two models require exhaustive connectivity (to account for arbitrary saccade directions and amplitudes), and each feature map would connect to each priority map separately. Moreover, transient post-saccadic connection shifts must be postulated to return to default retinotopic connections upon saccade landing. (3) Neural remapping results from horizontal transfer of activity in the priority map with no changes in connectivity. A top-down connection (attention pointer) produces attentional benefits [2]. In all three scenarios, neuron #2 is active after the saccade, sustaining attention at the location in space that previously contained the flashed stimulus. Abbreviations: LIP, lateral intraparietal area; FEF, frontal eye field; SC, superior colliculus; RF, receptive field.

before saccade, they found two different RF spatial profiles depending on the time of recording relative to the saccade and on the location of the pre-saccadic RF with regard to the direction of the saccade goal. In particular, for neurons with pre-saccadic RFs in the hemifield opposite to the saccade goal, they found clear activity at the remapped location of the RF of the cell approximately 150 ms after the saccade. By contrast, neurons with RFs in the same hemifield as the saccade target more often became selective for the vicinity of the movement goal, approximately 300 ms after the saccade. These findings may reconcile 'classical' remapping responses [1], with the results supporting the alternative account [6,7]. Moreover, they suggest that for stimuli flashed just before the eyes move, the signature of remapping takes time to become apparent. This delay is indeed expected if remapping depends on attentional mechanisms. Although the observed response patterns were complex, these results show remapping in a feature map, provided enough time is available for updating to occur in the priority maps.

Perhaps the most critical test of the theory of updating of attention pointers goes beyond the spatial profile of the RF. In a recent study, Yao and colleagues [9] provide the first neural evidence for a transfer of attentional states across saccades. While recording the activity of neurons in the motion-sensitive area MT (feature map), they presented a spatial attention cue either in the future (post-saccadic) location of the RF of a neuron or in a control location. Following that cue, two patches of moving dots appeared, with one in the post-saccadic RF – thus either coinciding with the cued (attended) or the control location (unattended). In their critical condition, the monkey prepared a saccade and the motion patch disappeared before the eyes started moving. Although the stimulus was purely presaccadic and never appeared in the RF, MT neurons showed a clear remapping response. Importantly, this memory trace of remapping was enhanced by a top-down attentional modulation established before the saccade. Moreover, this effect did not require a match between the direction of motion in the pre-saccadic stimulus and the direction preference of the MT neuron. These results support key predictions of the theory of remapping of attention pointers: the existence of horizontal transfer of attentional states that are selective for location. The signals driving these effects are likely to originate in priority maps that have little selectivity for features.

Together, these studies reestablish 'remapping' as a mechanism for visual stability and suggest a key role of attentional top-down processes. Importantly, they support a link between neural and behavioral evidence of remapping through a simple attentional mechanism (Figure 1): horizontal transfer of activity in priority maps (LIP, FEF, and SC) increases sensitivity at the remapped locations of attended stimuli in feature maps, enabling trans-saccadic tracking of attended targets [4]. This exciting work provides key insights into the link between remapping and attention, taking us two steps further in our endeavor to understand visual stability.

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Forum

Feature-Based Attention and Feature-Based Expectation

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Foreknowledge of target stimulus features improves visual search performance as a result of 'feature-based attention' (FBA). Recent studies have reported that 'feature-based expectation' (FBE) also heightens decision sensitivity. Superficially, it appears that the latter work has simply rediscovered (and relabeled) the effects of FBA. However, this is not the case. Here we explain why.

Attention can prioritize the processing of stimulus features (e.g., red) or dimensions (e.g., color). This 'feature-based attention' (FBA) has been most intensively investigated using visual search paradigms. Consider a search task in which observers view several dot motion patches, and are asked to detect which one is moving coherently (Figure 1A). Feature-based cues providing valid foreknowledge of the target motion direction (e.g., 45°) facilitate detection performance relative to neutral or invalid cues [1,2].

A distinct line of research has investigated how expectations about features influence behavior and modulate brain activity [3]. Consider a discrimination task in which observers view two dot motion patches, and are asked to report whether the motion direction in one patch (e.g., right of fixation) is clockwise (+45°) or counterclockwise (−45°) of vertical (Figure 1B). When cues signal the expected direction of dot motion (e.g., +45°), observers can combine this prior knowledge with visual feature information. This leads to an overall increase in accuracy.

This advantage for expected features on the discrimination task seems wholly consistent with FBA, exactly as facilitation in search tasks seems to follow naturally from expectations about the target feature. Superficially, it may thus appear that these two manipulations (which, in our example, both cue an expectation of +45° motion) simply index the same attentional process. Here, however, we argue that this is not the case. Instead, we draw a distinction between manipulations (i) that provide information about the relevance of