

to study by using traditional methods and will lead to a much more detailed understanding of silent and place cells and the nature of sparse coding in the brain.

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Allocating Attention in Rank-Ordered Groups

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When confronted with multiple stimuli, it is often necessary to prioritize one’s attentional resources. In this issue, Lennert and Martinez-Trujillo (2011) investigate the neural dynamics in dorsolateral prefrontal cortex for stimulus pairs of differing importance and demonstrate that the responses to the lesser stimuli become increasingly suppressed with increasing difference.

Primate groups tend to organize themselves in hierarchical structures where each individual has a specific social rank. It has been well documented that in such groups, high-rank individuals tend to receive more attention than low-rank individuals (Chance, 1967). It is clearly useful to keep an eye on high-rank individuals during social encounters because even small communication signals they send out might have large consequences for one’s own well-being. Because direct staring is generally interpreted as a dominant and aggressive gesture (Emery, 2000) much of the attention to high-rank individuals is paid covertly without directing gaze toward them. But how does rank order affect the neural mechanisms that subservise covert attention?

In this issue, Lennert and Martinez-Trujillo set out to answer this question (Lennert and Martinez-Trujillo, 2011), taking as a starting point findings linking activity in the dorsolateral prefrontal cortex, as well as the closely related frontal eye fields

(FEF), to control signals that regulate attention allocation in more posterior brain regions (Buschman and Miller, 2007; Moore and Armstrong, 2003). In their task, they did not study social rank, but instead they had monkeys learn a hierarchy among a set of colored moving random dot patterns. Patterns were presented side-by-side, one to each visual hemifield, and monkeys had to detect a small change in the movement direction of the higher rank pattern to obtain a reward while ignoring a change in the lower rank pattern. Monkeys readily learned the rank of the individual patterns by trial and error throughout the course of a training period, which is consistent with a known tendency of monkeys to remember elements in an ordered list by their list rank (Orlov et al., 2000). As a critical control, a new pattern was introduced once the hierarchy had been well learned, and monkeys were indeed able to use transitive inference ($A > B$ and $B > C$ implies that $A > C$) when faced with this new pattern. This confirms

that monkeys had in fact learned a hierarchical structure among the patterns rather than memorizing the appropriate response for all stimulus combinations.

For the recording of neural activity in the dorsolateral prefrontal cortex, they introduced a small but important modification: the presentation of the two stimuli of different rank to each visual hemifield was preceded by presentation of two gray neutral random dot patterns, with no—or therefore indeterminate—rank in the same location of the visual field. These neutral patterns served as placeholders and the actual attention task began only with a color change of these patterns. For the prefrontal cortex, the presentation of these neutral stimuli already evoked robust activity. Their single neuron example quadrupled its activity to these neutral patterns and across the population activation was approximately doubled. If one accepts the notion that these prefrontal activities are related to attentional control in posterior cortices, this enhancement to the

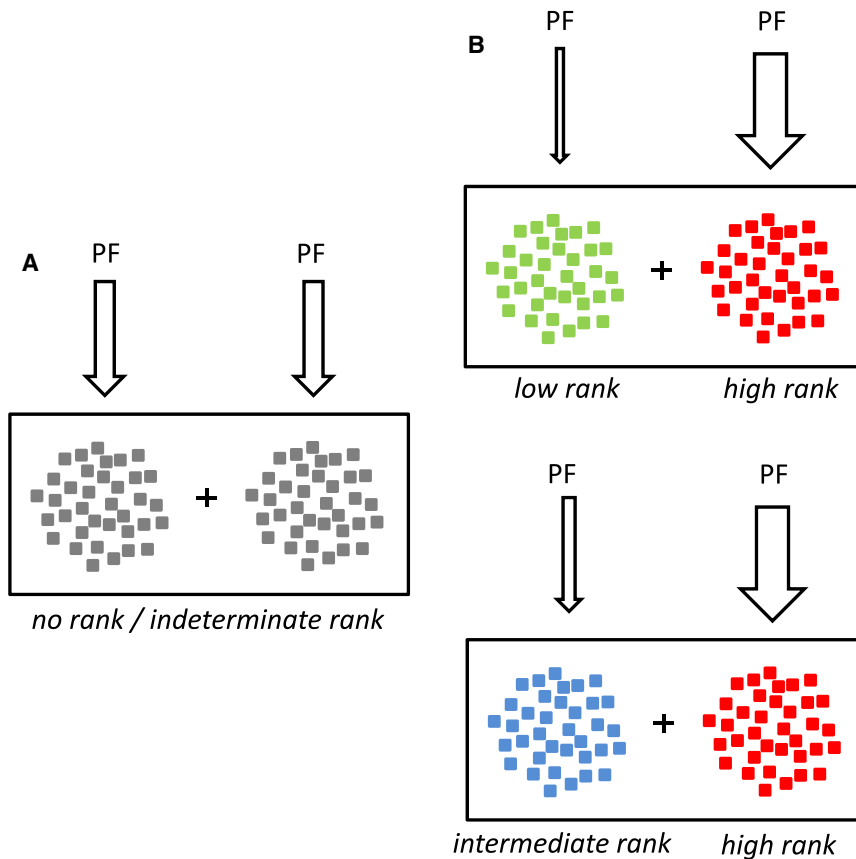


Figure 1. Prefrontal Attentional Activity Modulation by Stimulus Rank

(A) PF neurons are active to neutral patterns prior to the color switch, reflecting allocation of attention. (B) PF activity reductions are correlated with rank distance between the two competing patterns, whereas activity enhancements are not. Arrow size represents PF neural activity strength.

neutral stimuli signifies allocation of attention to each of the two patterns in nearly equal amounts (see Figure 1, left panel). This makes a lot of sense because the high-rank pattern will appear with 50% probability at each of these two locations. With a color change, the neutral patterns were replaced with two patterns that differed in hierarchical rank and the higher rank pattern had to be further attended in order to allow detection of a small change in movement direction of the random dots. When the higher rank pattern fell inside the receptive field of the recorded neuron, this neuron responded with increased activity. This is the anticipated result in the context of attentional selection theories, which posit that enhanced activity leads to a bias in competition between multiple stimuli competing for attention (Desimone and Duncan, 1995). When the higher rank pattern fell outside of the neuron's receptive field a reduction in activity was

observed consistent with the idea that the lower rank stimuli within the receptive field is losing the attentional competition.

The novel and surprising aspect of the results becomes apparent when one compares neural activity to pairs of patterns as a function of rank difference. The logic behind this is that attentional selection for large rank differences is an easy problem, because it is quite clear which stimulus has higher rank. By contrast, selection for stimuli with adjacent rank is a harder problem and the attentional competition can be expected to be more difficult. Rank difference indeed did have an impact on prefrontal neural activity: surprisingly, however, it only affected the reductions of neural activity seen in response to lower rank patterns. The enhanced activity observed for higher rank patterns did not depend on rank differences between the two patterns competing for attention (see Figure 1, right panels).

These findings are intriguing because they show that it is reductions, not increases, in activity that correlate with attentional performance differences based on the rank difference between the stimuli. The larger the rank difference, the clearer is the outcome of the competition between the two stimuli and the greater are the reductions of prefrontal activity relative to the baseline activity to the neutral stimuli. The activity reductions thus correlate better with behavioral performance and probably provide a more accurate account—compared to activity enhancements—of how the prefrontal cortex coordinates attention in posterior brain areas when multiple stimuli compete for attention. It is important to remember in this context that the activity reductions occur from an elevated level of activity evoked by the presentation of the neutral stimuli preceding the attentional competition so it is not clear at present whether we are dealing with reduced excitation or the consequences of inhibitory circuit activation in the prefrontal cortex. This issue can be experimentally addressed by pharmacological experiments, for example, by involving blockade of inhibition. It is however known that inhibition plays a central role in generating stimulus selectivity in other parts of the visual system (Shapley et al., 2007; Wang et al., 2002), suggesting that it may also be at work in the prefrontal cortex to generate highly selective control signals suitable for modifying information flow through posterior cortical areas.

In the present study, the two competing patterns were presented to opposite visual hemifields close to the fovea in an area spanning from 4° to 8°. Recordings were performed in one hemisphere of the brain, and the location of the high-ranking and low-ranking stimuli were varied to generate situations in which each of them fell in the receptive field under study. The competition between the two stimuli is thus inferred rather than directly measured. It is known that visual sensitivity of neurons in the prefrontal and FEF cortices emphasizes the opposite visual hemifield (Rainer et al., 1998; Suzuki and Azuma, 1983) so that one could obtain simultaneous information about neural signals related to the higher ranked and lower ranked patterns by bilateral recordings from both brain hemispheres. This would also allow the

investigation of how activity to attended and unattended stimuli evolve on a trial-by-trial basis. In particular, one could then examine whether there is indeed a close relationship between the dynamics of neural activity in the two representations in the two hemispheres as would be predicted based on competitive interaction models of attention.

How are these experimental findings now related to the social encounters in hierarchical groups alluded to in the beginning of this preview? During an encounter with two individuals of similar rank the representation of the lower ranked individual will be relatively weakly suppressed. Although the lower ranked individual will receive less attention than the higher ranked individual some re-

sources will still be devoted to keeping an eye on this group member. After all, his or her actions might have a relevant impact on the observer. For large rank differences, attention is again devoted to the high-rank individual, but now all resources are removed from the low-ranking individual. Thus, the main impact of rank difference is not how much we focus on the dominant group member, but to what extent we ignore other group members nearby.

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