Commentary on Moran and Desimone's 'spotlight in V4'

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Moran and Desimone's article entitled "Selective attention gates visual processing in the extrastriate cortex" (1985) is often cited as providing neurophysiological evidence for the spotlight theory of attention. This is not surprising, since in the article the authors claim that "attenuation of irrelevant information can be based purely on spatial location," and that "the effect of the unattended stimulus is attenuated, almost as if the receptive field has contracted around the attended stimulus". The results reported in this influential article, however, are ambiguous. The following commentary is meant to explain how the results can be reinterpreted along other lines that are currently available in the literature. This is important since the findings are frequently taken as evidence of spatial selectivity within a receptive field (something the data do not unequivocally demonstrate) and also form the basis for some recent computational models (e.g., Olshausen, Anderson, & Van Essen, 1993).

Moran and Desimone used a modified version of a delayed match-to-sample task. In their version, two colored oriented bars were presented at different locations in a cell's receptive field at both sample and test. The monkey's task was to attend to the bars appearing in only one of the two locations. When the test stimulus was identical to the preceding sample at the attended location, the animal was rewarded with a drop of water if it released the bar immediately, whereas when the test stimulus differed from the sample at the attended location, the animal was rewarded only if it delayed release for 700 ms. They found that the locus of the animal's attention within a cell's receptive field correlated strongly with the cell's response. In particular, when an effective stimulus and an ineffective stimulus were both present in a cell's receptive field and the animal attended to the effective stimulus, the cell responded relatively strongly. However, when the animal attended to the ineffective stimulus, the response was attenuated. The measure of selective attention used was an "attenuation index (AI)". The magnitude of the AI was calculated by dividing the response to the stimuli when the animal ignored the effective stimulus by the response to the same stimuli when the animal attended the effective stimulus.

In the first design that Moran and Desimone used, the effective stimuli at one location in the receptive field always differed in some sensory quality, such as color, from the ineffective stimuli at the second location. Thus, as the authors noted, there are two possible interpretations for finding a reduced response when the animal attended the ineffective stimuli— either a spatial or a featural explanation. In the former case, the animal's attention to a particular location would cause the receptive field of the cell to contract around this attended location and hence the cell would not respond to effective stimuli in another part of its receptive field. Alternatively, attention might affect neuronal responses based on stimulus dimension. For example, for a cell that preferred red, the act of attending to and remembering red might enhance the cell's response to the stimuli in its receptive field, whereas the act of attending to and remembering green might attenuate the cell's response to the same stimuli.

Several reports on the neurophysiology of attention have demonstrated effects related to feature selective attention. Detailed studies have documented changes in cell response in V4 and IT that are dependent on what stimulus properties the monkey is searching for. Most of these studies have used delayed match-to-sample tasks similar to that used by Moran and Desimone.

An early report by Fuster and Jervey (1982) neatly illustrates the featural interpretation of the Moran and Desimone study. Like Moran and Desimone, Fuster and Jervey recorded from IT cells during a color match-to-sample task. A trial began with the presentation of the sample (a colored light). After a delay, four colors appeared simultaneously at test. Choosing the color that matched the sample color was rewarded. The sample color and its position in the choice array were changed at random from trial to trial. They reported effects related to the color being remembered. For example, if a cell responded strongly for red stimuli presented within its receptive field, its response to the array of test stimuli was enhanced following red samples and attenuated following green samples, even though the test stimuli were identical. Thus, cell response changed depending on the sample presented. In their experiment, the attenuation was not due to location, since the stimuli appeared in random positions. Depending on one's viewpoint, one may label this modulation of cell response as some sort of selective attention to stimulus features or, as do Fuster and Jervey, as short term visual memory. Haenny, Maunsell, and Schiller (1988), and Maunsell, Sclar, Nealey, and DePriest (1991) report a similar modulation of cell response in area V4 for orientation match-to-sample tasks.

Most of the data described by Moran and Desimone was collected with the effective and ineffective stimuli in fixed locations. Thus, location was confounded with stimulus feature. They do report a second design, where they claim to test whether attenuation could be based on spatial location alone. To accomplish this, the locations of the effective and ineffective sensory stimuli were switched randomly. In this design, they report that the responses of cells were still determined by the stimulus at the attended location: cells responded well when the effective sensory stimulus appeared at the attended location and poorly when it appeared at the ignored location. From this they conclude that attenuation of irrelevant information can be based purely on spatial location in V4 and IT cortex. However, much of the effect was eliminated in the second design, suggesting that the effect was in fact largely depending on features— a finding not dealt with in the article.

Further, it is crucial to know whether there was an attenuation at both sample and test in the second design, or whether the attenuation is mainly occurring at test and therefore possibly due to attention to stimulus features and not location. As discussed above, cell response in V4 and IT cortex is modulated by what feature the animal is looking for in delayed match-to-sample tasks. Given that the Moran and Desimone task required the animal to attend to the color or orientation of the sample, it is not possible to know whether the attenuation in response that they report is due to attention to stimulus features alone or whether, in addition to this, there is an attentional effect of location. It is arguable that the data from Moran and Desimone's second design obtained during the very beginning of the sample period (i.e., the time before the monkey knows the sample color) is free from the possible confound that the attenuation is just due to the fact that the animal was searching for a particular color or orientation. However, the only data that are clearly reported to be obtained using the second design are not graphed and the AI is reported as combined AI for the sample and test stimuli.

It remains to be demonstrated whether or not there is attenuation of cell response to effective stimuli within the receptive field of cells in the temporal pathway that is based purely on spatial location. This spatial attenuation must be clearly disambiguated from selection based on stimulus features. Such selection to stimulus features can be occurring at a task level (as was the case in Moran & Desimone's first design) or at the level of an individual match-to-sample trial (as others have shown, see e.g., Fuster & Jervey, 1982, Haenny et al, 1988; Maunsell et al, 1991).

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