How the brain pays attention to others' attention

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Humans and other primates have evolved skills to interpret and respond to highly complex social information. This ability is reflected in multiple cortical regions of the macaque brain devoted to the visual analysis of individuals (1, 2), actions (3, 4), and scenes (5). Beyond visual analysis, social perception engages brain areas that govern an observer's strategic examination of stimuli (6), for example directing attention to scene elements with the most relevant social information. Consider a monkey sneaking a cautious glance at a gathering of other monkeys (Fig. 1*A*). There exists information about many social variables: who is there, how they are feeling, why they are gathered, and what might happen next, to name a few. One's capacity to retrieve information is limited, and an observer must prioritize information that is of immediate relevance. How does the brain implement the selective attention to pertinent social information? An important clue comes from a recent electrophysiological study by Ramezanpour and Thier (7), who discovered that neurons in a specialized region of the macaque cerebral cortex become much more sensitive to the gaze direction of an observed face when the subject actively seeks that information.

Based on previous work from the same group (8), Ramezanpour and Thier had a strong clue that such neurons might exist within a small patch on the floor of the superior temporal sulcus (STS). Functional MRI experiments showed that this area was uniquely activated when a subject actively tried to determine where a face was looking (Fig. 1*C*, *Inset*). Residing outside of the well-studied face-patch network (9), this region is relatively unexplored but in the vicinity of other STS areas recently described as having a role in selective attention (10–12).

To isolate this active component of face gaze analysis, Ramezanpour and Thier (7) designed a behavioral paradigm in which monkeys repeatedly viewed 16 macaque face images, each composed of a unique combination of four identities and four gaze direction. On each trial, the monkey was randomly assigned one of two behavioral tasks based on a small central color cue at the start of the trial. In the gaze-following task, the monkey was required to attend to the gaze direction of the viewed face (Fig. 1*B*, *Inset*). Four dots were put onto the screen, with one of the dots matching the gaze direction of the viewed face. The subject then indicated the gaze direction of the viewed face by targeting its own eyes to the same dot. This action was monitored by an eye-tracking system. In the face identity task, the stimuli were identical, but the monkey ignored the gaze direction and instead reported the identity of the viewed face. In this case, the monkey directed its eyes to one of four prelearned positions corresponding to the four face identities. For each recorded neuron, Ramezanpour and Thier (7) were thus able to compare the activity to the same stimuli and to the same actions under two different attentional conditions: gaze-following or identity recognition.

Ramezanpour and Thier (7) found that the activity of many neurons throughout the gaze-following patch depended strongly on which of the two social variables were being monitored. The highest proportion of neurons were sensitive to gaze direction and became tuned during the gaze-following task. These neurons lost their tuning for the same stimuli and actions when the monkey attended to identity. For some neurons, this effect was evident even before any face stimuli appeared, and as soon as the monkey was cued about the task rule. The task dependence of the activity was most obvious when neural activity level was ranked based on the position tuning in the gaze-following task (Fig. 1*C*). The strong tuning for target position during gaze following all but disappeared when the monkeys performed the identity task. A much smaller proportion of neurons, which were spatially intermingled with the first, showed the converse pattern, responding only when monkey attended to the identity of the image. The activity of both populations appeared specifically concerned with faces, since a control condition involving symbolic shapes did not yield similar tuning. Outside this gaze-following patch, face-selective neurons

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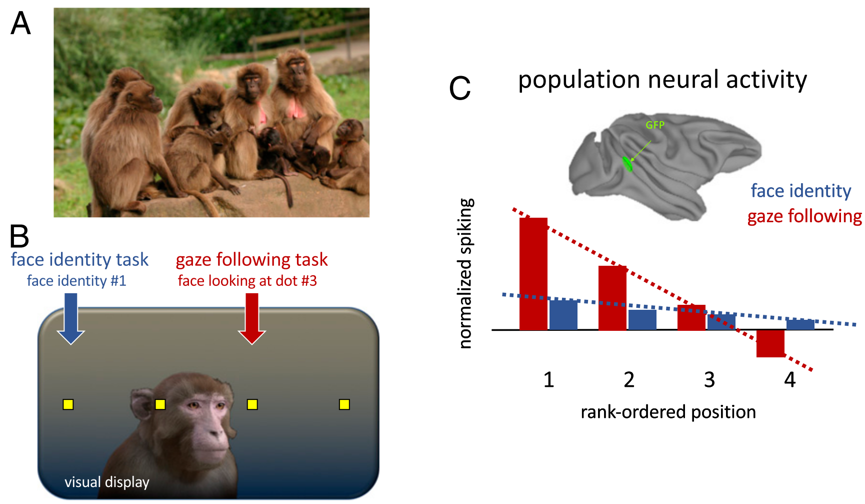

Fig. 1. (*A*) Natural scene of interacting baboons. Image courtesy of Pier Francesco Ferrari (photographer). (*B*) Description of the two tasks used by Ramezanpour and Thier. In both tasks, a macaque face was presented on the screen and four dots appeared in the foreground. In the gaze-following task, the monkey was required to attend to the gaze direction of the face and then direct its own gaze to the dot where the display face was looking (red arrow). In the face identity task, for the same stimulus the monkey was required to direct its gaze to a prelearned position associated with the particular identity (blue arrow). (*C*) Description of population neural activity. Under the gaze-following task, many cells responded more strongly and selectively to a subset of gaze target locations. When the responses were ranked and then compared to the face identity condition, responses showed notably less discrimination among the targets. (*Inset*) Approximate location of the gaze face patch (data from ref. 8).

were abundant, but their activity was minimally affected by the two different attention conditions.

The findings are important foremost because they provide clues about how the visual brain supports the faculty of joint attention, which is a critical ingredient in the complex, hierarchical world of primates (13, 14). They nicely complement recent recordings from the macaque amygdala, which also found a dependency of single neurons on gaze direction, in that case related to the establishment of eye contact (15). The STS is known to be replete with neurons responsive to stimulus features that may be relevant to gaze direction, including head orientation (16) and social interactions (17). However, to date these responses have been considered part of an advanced structural analysis of faces and scenes, with little notion that they are subject to strong modulation tied to task relevance. It is also noteworthy that the gaze-following patch occupies a part of the STS that is thought to receive relevant visual and attention-related input through pathways involving the superior colliculus and thalamic pulvinar (18). In fact, a recent set of experiments demonstrated that attentional modulation in a nearby STS region is causally dependent on activity in the superior colliculus (19). This visual pathway is closely linked to visual orienting and other forms of spatial attention (20). It is interesting to speculate that this subcortical route, which has been shown to have some involvement in face processing (21), might contribute to the attentional shaping of gaze direction responses in the STS.

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