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Neuropsychological evidence of a third visual pathway specialized for social perception

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Recent evidence suggests the existence of a neural pathway specialized for social perception projecting between the well-established "what" and "where" pathways. A new study of neuropsychological patients demonstrates that this social pathway is causally essential for recognizing dynamic facial expressions.

Understanding the behavior of other people

Humans are social primates living in a world of limited resources. This means that our happiness, our success and sometimes our very survival are dependent on successfully interpreting the actions and behavior of other people. The fundamental importance of social interaction in our lives is demonstrated by the existence of brain networks that are dedicated to understanding others[1]. This makes researching how the brain transforms sensory input into an accurate cognitive representation of another person a fundamental challenge for neuroscience. One of the most theoretically productive approaches in pursuit of this goal has been to map the anatomical and functional connectivity of the visual cortex. A new study by Prabhakar and colleagues[2] published in Nature Communications examines the hypothesis that the brain contains a specialized neural pathway for visual social perception. They tested a large group of neuropsychological patients ($N = 108$) with focal brain lesions in different parts of the visual cortex. The results demonstrated a double dissociation in the recognition of moving and static facial expressions that was determined by lesion location. These findings are consistent with the recently proposed third visual pathway for social perception that projects along the lateral surface of the brain[3].

Finding and recognizing objects

Influential models of primate visual cortex (Fig. 1) proposed two anatomically segregated neural pathways specialized for the 'what' and 'where' of visual object recognition[4,5]. The ventral pathway runs along the bottom surface of the brain and is specialized for visually identifying an object (e.g., "Is that an apple or an orange?"). The dorsal pathway runs along the top surface of the brain and is specialized for identifying the location of an object and for reaching out and grasping that object (e.g., "Pick up the apple on the left!"). The original conception of the two visual pathway model was based on neuropsychological studies of human and non-human primates[4–6]. Dissociable behavioral impairments were observed in both species following damage to the temporal cortex (in the ventral pathway), or to the parietal cortex (in the dorsal pathway). Temporal lesions impaired visual object recognition tasks but spared visual object location and object grasping tasks. Parietal lesions impaired visual object location and object grasping tasks but spared visual object recognition tasks. This type of double dissociation is taken as strongest pattern of results in neuropsychology[7] and the studies cemented the two pathways as one of the fundamental models of primate visual cortex[4,5].

People are not objects

Despite the importance of the two visual pathway model, there are some obvious limitations. Perhaps most notably, it cannot account for how we understand the actions and behavior of those around us. Other people are not inanimate objects that will remain passive if we reach out towards them, regardless of whether we can accurately identify them or not. Any social interaction is a qualitatively more complex process than simply locating another person in visual space and recognizing them. People respond to our actions and their behavior will continue to change and develop in response to our subsequent actions. One region of the brain in particular, the superior temporal sulcus (STS), computes the sensory information that facilitates these cognitive processes[8,9]. The study from Prabhakar et al.[2] aims to better understand the behavioral functions of the STS by dissociating social perception from visual object recognition. They did this by testing neuropsychological patients with damage to either the ventral pathway (for object recognition) or damage to the STS (for social perception).

The STS preferentially responds to moving biological stimuli (e.g., faces and bodies) and computes the visual social cues that help us understand and interpret the actions of other people. These include facial expressions, eye gaze, body movements and the audio-visual integration of speech[8,9]. Visual motion is crucial for all these functions because it can act as the cue for a change in the behavior, mood and intentions of another person (e.g., a smile that changes into a frown). The STS responds more strongly to moving faces than to static faces, while face-selective areas in the ventral pathway show a greatly reduced, or no difference in the response to moving and static faces[10]. In addition the STS shows little or no neural response to objects and visual scenes regardless of whether they move or remain static[11]. This selective response for moving biological stimuli in the STS led to the recent proposal of a third visual pathway specialized for social perception[3].

Learning Lessons from Lesions

Prabhakar et al.[2] tested the veracity of the third visual pathway in a study of neuropsychological patients who were asked to recognize either moving or static facial expressions. Patients with lesions encompassing the STS (but not the ventral pathway) were impaired at recognizing moving facial expressions but were relatively unimpaired at recognizing static facial expressions. By contrast patients with lesions to the ventral pathway (but not the STS) were impaired at recognizing static facial expressions but relatively unimpaired at

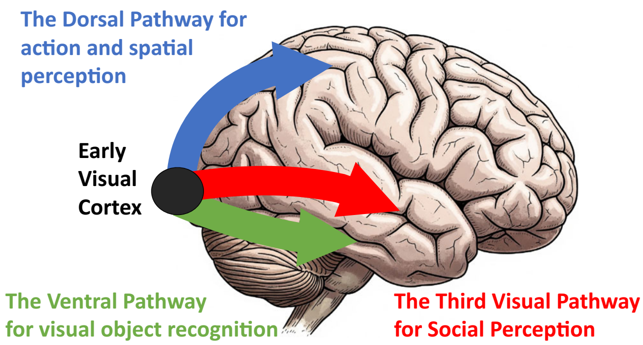

Fig. 1 | The three visual pathways. A schematic representation of the three visual pathways that project from early visual cortex. Prior models of primate visual cortex proposed two pathways[4,5]. A ventral or "what" pathway (shown in green) for visual object recognition, and a dorsal or "where" pathway (shown in blue) for locating objects in visual space and performing visually guided physical actions. The original empirical data that supported these models was derived from neuropsychological studies of human and non-human primates[4,5]. A recent update has proposed a third visual pathway on the lateral brain surface[3]. This third pathway (shown in red) is specialized for processing the dynamic visual information that supports social perception. The study by Prabhakar and colleagues[2] published in Nature Communications provides causal evidence of the existence of this third visual pathway. They do this by testing a large group of neuropsychological patients ($N = 108$) with focal brain lesions in different parts of the visual cortex. Results showed a double dissociation in the recognition of moving and static facial expressions that was determined by lesion location. STS lesions preferentially impaired moving expression recognition, ventral lesions preferentially impaired static expression recognition. These results are consistent with the proposed role of the third visual pathway for social perception[3].

recognizing moving facial expressions. This double dissociation in moving and static expression recognition is consistent with the proposed role of the third visual pathway in social perception[3]. The impairment in recognizing moving facial expressions in the patients with STS lesions was distinct from general visual motion processing impairments. This is important because the third pathway includes the motion-selective area V5/MT. V5/MT responds to any type of visual motion (e.g., moving dots, bodies, objects, faces) and is an established component of the dorsal pathway[5]. It was therefore crucial to show that STS lesions selectively impaired the recognition of only moving biological stimuli and not the recognition of any type of visual motion.

Prior to the advent of neuroimaging the detailed study of behavioral impairments resulting from focal brain damage was one of the few experimental methodologies for understanding the functional organization of the human brain. Studies of neuropsychological patients produced unique insights into human cognition and brain organization[12], but have not been without controversy. For example, in neuropsychological studies it is unclear if the observed behavioral impairments result solely from damage to the lesioned brain area, or if the lesion causes widespread disruption across brain networks that perform a range of cognitive functions[13]. This is partly because patients with selective deficits are extremely rare and may not be representative of the wider population. Most patients with brain damage are impaired on a wide range of behavioral tasks and do not exhibit selective cognitive deficits. In addition, brain lesions occur randomly and therefore vary in location, size, and shape across each patient. Prabhakar et al.[2] were able to address these issues because they combined detailed behavioral testing with structural neuroimaging data in a convincingly large group of patients ($N = 108$). Mapping brain damage using multivariate lesion-symptom mapping in such a large group can begin to account for the individual differences in lesion size and location. This greatly strengthens the veracity of their conclusions in attributing specific behavioral impairments to anatomically dissociable brain areas.

Study structure to understand function

Hierarchical models of brain function link anatomically connected brain areas with distinct functional responses to explain how cognition evolves from basic sensory inputs[13]. Visual information from the eye is relayed to primary visual cortex (V1) before feeding forward to higher brain areas that respond to increasingly complex visual features (Fig. 1). Prabhakar et al.[2] performed additional analyses to demonstrate the dissociable anatomical connections that dissociate the ventral pathway from the social perception pathway[3]. The precise lesion locations in each patient were taken from structural brain scans and then mapped to the white matter tracts that would typically connect these areas in the undamaged brain. Results showed the STS lesions that produced moving expression impairments were anatomically dissociable from the ventral lesions that produced static expression impairments. STS lesions were associated with the right middle longitudinal fasciculus and arcuate fasciculus. While ventral lesions were associated with the inferior longitudinal fasciculus and inferior fronto-occipital fasciculus. This result neatly links the behavioral impairments resulting from the lesioned cortical areas to the white matter connections that anatomically dissociate the ventral and third visual pathways.

Cajal stated that "All natural arrangements, however capricious they may seem, have a function". Characterizing the visual system as distinct neural pathways enables researchers to construct hierarchical models of cognitive function that are informed by neuroanatomical connectivity. This linking of structure and function facilitates understanding between researchers who study different species[3–5,8], different stages of development[10,11,14] and use different experimental methods[6,9–11,15]. The study from Prabhakar et al.[2] is a significant contribution to the body of empirical research demonstrating the functional and anatomical dissociations between the putative visual pathways. Their study reports behavioral and neuroimaging data from a large group of patients that would not have been possible forty years ago. This takes the visual pathway research literature neatly back to its neuropsychological origins[4–6] while simultaneously addressing innovative and fundamental questions about brain organization.

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