**Title**: Visual Neuroscience: A specialised neural pathway for social perception

**Author Name:** David Pitcher

**Summary:** Humans are an intensely social species. Our daily lives depend on understanding the behaviour and intentions of the people around us. A new study identifies a neural pathway specialised for interpreting the physical actions that we use to understand others.

**Main Text:** Explaining the neural processes that enable us to see and interact with the people, places and objects we encounter in the world is a fundamental aim of visual neuroscience. A rich theoretical approach in pursuit of this goal has been to show that dissociable cognitive functions are performed in anatomically segregated neural pathways 1,2. These models propose that the cognitive functions performed in a particular brain area can be deduced (at least partially) from the anatomical connectivity of that area. In this issue of *Current Biology* McMahon et al 3 use a condition-rich neuroimaging experimental design to investigate how humans recognise and process socially relevant visual information. Their results demonstrate the existence of a hierarchical neural pathway specialised for understanding the socially relevant actions of other people.

Foundational models of the primate brain proposed two functionally distinct hierarchical pathways projecting from primary visual cortex to higher brain areas 1,2. A ventral pathway specialised for visual object recognition, and a dorsal pathway specialised for performing visually guided physical actions (Figure 1). However, as neuroimaging techniques have improved it has become increasingly clear that these models need to be updated. Specifically, neither pathway can account for the neural mechanisms that underpin human social interaction. Social interactions are predicated on visually analysing the actions of others and responding appropriately. One brain area in particular, the superior temporal sulcus (STS), computes the sensory information that facilitates these processes 4-6. A recent model proposed that the STS is part of a third visual pathway on the lateral brain surface 7. This pathway is specialised for processing the dynamic visual input that underpins social interactions (Figure 1). Crucial to this model is the anatomical and functional connectivity between the STS and brain areas that respond to fundamental visual properties, most notably motion.

Motion is fundamental to social interaction. The diverse range of movements generated by faces and bodies (e.g., facial expressions, body language, the audio-visual integration of speech) are how primates understand each other 8,9. Quantifying this diversity in realistic stimuli using tractable experimental designs has been a significant challenge in visual neuroscience for decades. McMahon et al 3 have designed an innovative solution to this issue. They curated a data-rich set of 250 3-second videos depicting a range of social interactions between two people (e.g., two people doing Karate or two people reading a map). These videos have been annotated to identify visual features that should be selectively processed in brain areas at different levels of the visual hierarchy. These include low-level features (e.g., contrast and motion energy), mid-level features (e.g., physical distance between the actors and their direction of attention) and high-level features that support social understanding (e.g., the nature and valence of the interaction). Participants viewed these videos while being scanned with functional magnetic resonance imaging (fMRI). This enabled the authors to precisely map which brain areas responded to which visual features.

The results demonstrated a hierarchical organisation for understanding social actions along the lateral visual pathway. Low-level visual features (e.g., motion) were processed in early visual cortex and motion-selective brain areas 10. Mid-level features (e.g., features that convey the geometry of the scene) were processed in brain areas that selectively respond to bodies and objects 11,12. High-level features describing the nature of the social interaction and the intensity of the interaction were processed in higher brain areas along the STS 5,6. This mapping of simple to complex visual information (as depicted in the videos) onto brain areas that preferentially respond to this information empirically defines a neural hierarchy for social understanding. Importantly, these results functionally dissociate the lateral visual pathway (along the STS) from the established ventral pathway for object recognition and dorsal pathway for performing visually guided physical actions (Figure 1).

McMahon et al 3 have demonstrated an exciting new approach that bridges the fields of sensory neuroscience and social neuroscience. This opens up new ways to study the neural basis of social cognition and how it operates in both non-clinical and clinical populations. For example, individuals with autism show an impaired neural response in motion-selective visual areas, and impaired performance when performing behavioural motion discrimination tasks 13. This has led to theories proposing that the social impairments observed in autistic individuals may result from an impairment in prediction 14. Predicting the responses our behaviour will elicit in others is part of social interaction. Social interaction is informed, at least partially, by the non-verbal cues generated by the faces and bodies of the people around us. In autism, it is theorised that impaired motion perception leads to impaired prediction of these non-verbal cues, and this impairs the capacity to understand the intentions and feelings of others. Using more socially realistic and data-rich videos depicting social interactions will hopefully be able to identify the differences in processing dynamic social information in people with autism.

Social interactions are not only about understanding the intentions of other people, they also involve a decision about how to respond (even if that decision is to do nothing). Decision making suggests the involvement of brain areas higher in the cortical hierarchy than the STS, notably in the prefrontal cortex. Non-human primate studies report anatomical connectivity between the STS and the prefrontal cortex 15. More recent human neuroimaging studies have also demonstrated that the STS and the prefrontal cortex are functionally connected when processing moving faces 16,17. Consistent with this hypothesis McMahon et al 3 report activity in the prefrontal cortex. However, this activity was not reliably correlated with any of the visual features they identified in the video stimuli. Further characterising the role of the frontal cortex in visual action understanding is an important question for future studies.

The detailed mapping of visual information also reveals intriguing hemispheric differences at higher levels of the visual hierarchy. For example, the videos that depicted greater levels of communication (e.g., more social interaction and higher valence) were preferentially processed in the right hemisphere. Why should the visual information that supports social understanding be preferentially processed in the right hemisphere? One suggestion comes from a recent model of visual action perception that describes the neural basis of how humans interact with objects (e.g., grasping a tool) 18. This model proposes that action observation involving objects is primarily a left hemisphere function. A hemispheric dissociation between visual actions that support object use and visual actions that support social understanding is consistent with the findings of McMahon et al 3. While the reasons for this asymmetry are unclear, evolutionary theories have been proposed 19. One suggests that the higher-order cognitive functions that support behaviour unique to humans, such as spoken language, are preferentially processed in the left hemisphere. Anatomical studies show the planum temporale, a brain area adjacent to the STS that processes speech is larger in the left hemisphere 20. This division of function then allows the STS in the right hemisphere to preferentially process the nonverbal characteristics of faces and bodies that support social understanding. Future experiments that compare how non-verbal social information is differentially processed in human and non-human primates 19 can further address this question in future studies.

Charles Darwin famously identified two types of scientists: “lumpers” and “splitters”.

Lumpers look for the fundamental similarities that underpin the functionality of a system, splitters look to identify finer and finer differences between the components in a system. Defining cognitive functions that are selectively processed in anatomically defined neural pathways offers a conceptual approach that can bridge this division. Neuroimaging studies can be used to study the functions of specific brain areas (e.g., the motion-selective area or the STS) while simultaneously mapping the connectivity and broader functionality between these brain areas. Visual pathway models create the broader framework in which these results can be understood and interpreted. The results reported by McMahon et al in this issue of *Current Biology* 3 are an exciting new demonstration of this approach. Their study provides empirical support for the functional role of the lateral visual pathway while opening up many exciting and important questions for future study.

**References**

1. Ungerleider, L.G., and Mishkin, M. (1982). Two cortical visual systems. In D.J. Ingle, M.A. Goodale & R.J.W. Mansfield (Eds.) Analysis of Visual Behavior. In (Cambridge, MA: MIT Press), pp. 549–586.

2. Milner, A.D., and Goodale, M.A. (1986). The Visual Brain in Action (Oxford: Oxford University Press).

3. McMahon, E. (2023). Hierarchical organization of social action features along the lateral visual pathway. Current Biology *32*, xxx-xxx.

4. Perrett, D.I., Hietanen, J.K., Oram, M.W., and Benson, P.J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. Philos Trans R Soc Lond B Biol Sci *335*, 23-30. 10.1098/rstb.1992.0003.

5. Allison, T., Puce, A., and McCarthy, G. (2000). Social perception from visual cues: role of the STS region. Trends Cogn Sci *4*, 267-278. 10.1016/s1364-6613(00)01501-1.

6. Kilner, J.M. (2011). More than one pathway to action understanding. Trends Cogn Sci *15*, 352-357. 10.1016/j.tics.2011.06.005.

7. Pitcher, D., and Ungerleider, L.G. (2021). Evidence for a Third Visual Pathway Specialized for Social Perception. Trends Cogn Sci *25*, 100-110. 10.1016/j.tics.2020.11.006.

8. Jack, R.E., and Schyns, P.G. (2015). The Human Face as a Dynamic Tool for Social Communication. Curr Biol *25*, R621-634. 10.1016/j.cub.2015.05.052.

9. Vogels, R. (2022). More Than the Face: Representations of Bodies in the Inferior Temporal Cortex. Annu Rev Vis Sci *8*, 383-405. 10.1146/annurev-vision-100720-113429.

10. Watson, J.D.G., Myers, R., Frackowiak, R.S.J., Hajnal, J.V., Woods, R.P., Mazziotta, J.C., Shipp, S., and Zeki, S. (1993). Area-V5 of the Human Brain - Evidence from a Combined Study Using Positron Emission Tomography and Magnetic-Resonance-Imaging. Cerebral Cortex *3*, 79-94. DOI 10.1093/cercor/3.2.79.

11. Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., and Tootell, R.B.H. (1995). Object-Related Activity Revealed by Functional Magnetic-Resonance-Imaging in Human Occipital Cortex. P Natl Acad Sci USA *92*, 8135-8139. DOI 10.1073/pnas.92.18.8135.

12. Downing, P.E., Jiang, Y., Shuman, M., and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. Science *293*, 2470-2473. 10.1126/science.1063414.

13. Robertson, C.E., and Baron-Cohen, S. (2017). Sensory perception in autism. Nat Rev Neurosci *18*, 671-684. 10.1038/nrn.2017.112.

14. Sinha, P., Kjelgaard, M.M., Gandhi, T.K., Tsourides, K., Cardinaux, A.L., Pantazis, D., Diamond, S.P., and Held, R.M. (2014). Autism as a disorder of prediction. Proc Natl Acad Sci U S A *111*, 15220-15225. 10.1073/pnas.1416797111.

15. Kravitz, D.J., Saleem, K.S., Baker, C.I., and Mishkin, M. (2011). A new neural framework for visuospatial processing. Nat Rev Neurosci *12*, 217-230. 10.1038/nrn3008.

16. Wang, Y., Metoki, A., Smith, D.V., Medaglia, J.D., Zang, Y., Benear, S., Popal, H., Lin, Y., and Olson, I.R. (2020). Multimodal mapping of the face connectome. Nat Hum Behav *4*, 397-411. 10.1038/s41562-019-0811-3.

17. Nikel, L., Sliwinska, M.W., Kucuk, E., Ungerleider, L.G., and Pitcher, D. (2022). Measuring the response to visually presented faces in the human lateral prefrontal cortex. Cereb Cortex Commun *3*, tgac036. 10.1093/texcom/tgac036.

18. Wurm, M.F., and Caramazza, A. (2022). Two 'what' pathways for action and object recognition. Trends Cogn Sci *26*, 103-116. 10.1016/j.tics.2021.10.003.

19. De Winter, F.L., Zhu, Q., Van den Stock, J., Nelissen, K., Peeters, R., de Gelder, B., Vanduffel, W., and Vandenbulcke, M. (2015). Lateralization for dynamic facial expressions in human superior temporal sulcus. Neuroimage *106*, 340-352. 10.1016/j.neuroimage.2014.11.020.

20. Geschwind, N., and Levitsky, W. (1968). Human brain: left-right asymmetries in temporal speech region. Science *161*, 186-187. 10.1126/science.161.3837.186.

**Affiliation:** Department of Psychology, University of York, Heslington, York, YO10 5DD, U.K.

**Email:** david.pitcher@york.ac.uk

**Figure Legend Title:** The three visual pathways

**Figure Legend Caption Paragraph:** A schematic representation of the three visual pathways that project from early visual cortex. Prior models of primate visual cortex proposed two pathways 1,2. A ventral pathway (shown in green) for the visual object recognition, and a dorsal pathway (shown in blue) for performing visually guided physical actions. These pathways were predicated on the hypothesis that the function of a particular brain can be deduced (at least partially) by the anatomical connectivity of that area. A recent update has proposed a third visual pathway on the lateral brain surface 7. This third pathway (shown in red) is specialised for processing the dynamic visual information that supports social perception. The study by McMahon et al 3 reported in this issue of *Current Biology* provides empirical suport for the hierarchical structure of this third pathway from motion-selective visual cortex into the higher brain areas that support social cognition.