

AMAZING PAPERS IN NEUROSCIENCE

Faces in the Brain: The Discovery of a Neuronal Subpopulation Selective for Face Recognition

James Febery

School of Psychology and Neuroscience, University of St. Andrews, St. Andrews, UK KY16 9JP.

Facial recognition is a fundamental feature of primate social interaction. However, the location and number of neurons that are solely dedicated to the recognition of faces and facial features are not well known. The following mini review describes a paper by Perrett and colleagues that identifies and describes a subpopulation of neurons in the superior temporal sulcus that appear to be strongly tuned to faces and facial features. This paper holds great value for

undergraduate teaching, as it is a foundational paper within the literature of face recognition. It is an example of a publication that stands the test of time, promotes the birth of many new fields of research and displays easy to understand experimentation with profound results.

Key words: Face recognition; Superior temporal sulcus; subpopulation; Face selective; Facial Features.

Every day, we see and/or interact with others; this may be a stranger passing by, a family member at home, or a lecture hall full of students. This interaction, whatever the scenario, is heavily dependent on our ability to recognize faces. Facial recognition can be critical for survival in non-human primates (Boysen and Berntson, 1989; Nelson, 2001). However, the basic neural circuitry that allows for this seemingly simple task is not comprehensively described. A first account into this phenomenon identified the temporal lobe as an important area for facial recognition, due to neuronal activity being positively selective for facial stimuli (Perrett et al., 1979). Furthermore, a second investigation that focused on visual properties of neurons also identified the temporal lobe to contain neurons responsive to faces. However, these neurons were polysensory, and displayed activity in the presence of faces in addition to general arousing and aversive stimuli (Bruce et al., 1981).

Perrett and colleagues (1982) provide the first account of truly face selective neurons in the primate brain. The work is important for researchers because it is a comprehensive report on the location and number of strongly face selective cells. The publication also has value for educators as an example of a paper that can educate across multiple disciplines such as cognition, perception and research design classes.

Perrett et al. (1982) focused their investigation on identifying the location and number of neurons in the temporal lobe that are strongly selective to face and facial feature stimuli. The researchers identified a subpopulation of neurons strongly selective to faces and facial features in the superior temporal sulcus (STS) of rhesus monkeys. Their work laid the foundation for understanding the neural basis of face recognition.

The researchers performed extracellular neuronal recordings in rhesus monkeys from the STS, testing a total of 497 neurons for responses to facial stimuli. Figure 2 of the paper shows that 48 of the 497 neurons responded with up-to ten times greater activation to faces and facial feature stimuli in comparison to non-facial stimuli. The 48 neurons with this response profile were categorized as face selective neurons and were shown to have excitatory activation and response times that matched the duration of facial stimuli

presentation.

Figure 5 presents the first line of evidence suggesting that the 48 neurons were specifically facial feature and whole face selective. This was indicated first by their weak responses to basic geometric (high contrast images of gratings, bars and dots) and three-dimensional stimuli. When these neurons were presented with facial stimuli, their firing responses were ten times stronger in comparison to their responses to other images. Once the neurons were identified as face responsive, other modalities of sensory information were tested. This is because previously described face responsive neurons displayed firing activity when presented with various arousing and aversive stimuli (Bruce et al., 1981). Both auditory and tactile arousing and aversive stimuli were tested, and galvanic skin responses (GSRs) and single unit recordings monitored. Auditory stimuli of human voices and tactile stimuli of touching the leg resulted in large GSRs, suggesting that the subjects were strongly responding to the stimuli. However, the neuronal responses from the 48 neurons were very weak during presentation of these stimuli and did not match the level of activation that occurred with facial stimuli. Overall, the weak responses to arousing and aversive stimuli in the face responding neurons suggested that these stimuli did not strongly contribute to the responses seen in the presence of facial stimuli. Therefore, Figure 5 is significant because it highlights that a subpopulation of neurons are strongly selective to visual stimuli of faces and facial features but show little or no response to other stimuli. This type of highly selective response to faces had not been previously described in brain neurons.

The researchers next investigated how transformation of facial features modulated firing of these neurons. First the group investigated the role of color. They found that the neurons responded similarly to faces regardless of whether the faces were black and white or in color. This suggested that facial feature detection in these neurons was largely independent of color. Secondly, neuronal responses did not decrease when facial stimulus distance (20cm – 2m) and orientation of facial stimuli were changed.

Interestingly, Figure 8 presents how the neurons responded to changes in the profile of faces i.e., full-face at

0° through to side profile at 90°. A maximum response was seen with a full-face (0°) presentation. However, as the profile started to rotate towards side profile (90°), even as little as ten degrees, there was a marked reduction in neuronal response. This suggested that these neurons are tuned to fire maximally in response to full frontal views of faces. The next transformation investigated was facial features. The key question was, do these neurons respond to whole faces only or are there specific facial features that excite them? A series of facial stimuli were presented that had various facial features concealed from view. Overall, the majority of the neurons continued to respond with normal or very slightly diminished responses. However, for some neurons, a decrease in response was seen when particular facial features were concealed. For example, Figure 9 shows that eyes seemed critical for a small number of neurons to reproduce the same responses seen with the whole face. Perrett and colleagues found that 35 of the 48 face selective neurons displayed a preference to particular facial features, and without those features present, responses were weaker than with the whole face stimulus.

The investigation concluded that the individual responses of the face selective neurons to facial stimuli could not be accounted for by arousal or aversive stimuli. Furthermore, it is interesting to note that the majority of the neurons that were identified changed their activity in response to specific transformations of the facial stimuli. Both profile changes and concealment of facial features could diminish the response of a subpopulation of these neurons.

Critically, this publication was the first account of a subpopulation of neurons that are strongly selective, and therefore, tuned to visual stimuli of whole faces and facial features. It is, therefore, a foundational paper that launched many new areas of research. These include research into the selectivity of neuronal responses to facial features such as gaze direction, social signals and person perception within primates (Perrett et al., 1990; Perrett et al., 1992; Macrae et al., 2002). Furthermore, this paper was a basis for the discovery that face selective cells are a conserved phenomena shared between humans and non-human primates (Hoffman and Haxby, 2000; Haxby et al., 2002).

Finally, Perrett and colleagues made a connection between their neurophysiological discoveries and the neurological disorder of prosopagnosia, or face blindness. Prosopagnosia sufferers are unable to identify people when viewing their face but can still recognize objects. The disorder is linked to dysfunction in the inferior occipito-temporal region (Meadows, 1974). Perrett and colleagues hypothesized that the STS containing face selective neurons may provide vital information to the inferior occipito-temporal region, and that dysfunction in either the STS or the connection between the two regions may impair facial recognition and identification. This enhances the value of this paper for teaching as it provides a platform for discussing a unique neurological disorder, and it highlights how phenomena discovered with animal models might provide insight into specific neurological disorders.

AUDIENCE

This paper would be most suited for teaching 3rd and 4th year psychology and neuroscience undergraduate students. In particular, it could be used to aid research design classes, due to the paper demonstrating the use of relatively simple experimentation and systematic stimuli presentation to obtain interpretable results. This paper would also be well matched with perception classes as this work contributed to the foundations of our understanding of the neural basis of face perception. I suggest that this paper could also be of use in clinical psychology and cognition classes because of the link between the neurophysiological findings of this paper and the neurological disorder of prosopagnosia. Overall, the Perrett et al. (1982) paper investigates a fascinating topic in neuroscience, while remaining accessible to undergraduates and educators. This classic publication serves as an example of a paper that is adaptable to a range of teaching situations in psychology and neuroscience.

REFERENCES

- Boysen ST, Berntson GG (1989) Conspecific recognition in the chimpanzee (*Pan troglodytes*): cardiac responses to significant others. *J Comp Psychol* 103(3):215–220.
- Bruce C, Desimone R, Gross CG (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J Neurophysiol* 46(2):369–384.
- Haxby JV, Hoffman EA, Gobbini MI (2002) Human neural systems for face recognition and social communication. *Biol Psychiatry* 51(1):59–67.
- Hoffman EA, Haxby JV (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuro* 3(1):80–84.
- Macrae CN, Hood BM, Milne AB, Rowe AC, Mason MF (2002) Are you looking at me? Eye Gaze and Person Perception. *Psychol Sci* 13(5):460–464.
- Meadows JC (1974) The anatomical basis of prosopagnosia. *J Neurol Neurosurg Psychiatry* 37(5):489–501.
- Nelson CA (2001) The development and neural bases of face recognition. *Infant Child Develop* 10(1–2):3–18.
- Perrett DI, Rolls ET, Caan W (1979) Temporal lobe cells of the monkey with visual responses selective for faces. *Neurosci Lett* S3, S358.
- Perrett DI, Rolls ET, Caan W (1982) Visual neurones responsive to faces in the monkey temporal cortex. *Exp Brain Res* 47(3):329–342.
- Perrett DI, Harries M, Mistlin A, Hietanen J, Benson P, Bevan R, Brierley K (1990) Social Signals Analyzed at the Single Cell Level: Someone is Looking at me, Something Moved! *Int J Comput Psychol* 4(1):25–55.
- Perrett DI, Hietanen JK, Oram MW, Benson PJ, Rolls ET (1992) Organization and Functions of Cells Responsive to Faces in the Temporal Cortex. *Philos Trans R Soc Lond B Biol Sci* 335(1273):23–30.

Received March 09, 2018; revised May 23, 2018; accepted June 06, 2018.

The author would like to thank all involved in the University of St. Andrews MRes in Neuroscience program, and the program organizer Dr. Stefan Pulver.

Address correspondence to: James Febery, School of Psychology and Neuroscience, University of St. Andrews, St. Andrews, UK KY16 9JP. Email: jf99@st-andrews.ac.uk