The present findings align with the predictions of a dual-system model of decision making. However, there is a large number of possible models, few of which are excluded by these data. The rapid CdN decoding suggests that the value in the present task is unlikely to be constructed from more fundamental quantities, such as juice quantity and probability, at the onset of the pictures. As always, being able to decode a choice is not proof that the region guides the decision. And the question of whether value representation in any particular region happens pre- or post-decision remains—in many cases—a chicken and egg problem.

We cannot ask monkeys at which point they are aware of their decision but it is intriguing that, as in humans, a decision can be decoded long before a movement to respond is initiated. There are ample data suggesting that humans are unaware of their decisions when they are first made. Benjamin Libet's (Libet et al., 1983) finding of a 350-ms delay between decoding and awareness has since been extended to decoding decisions at least 10 s before awareness sets in in humans (Soon et al., 2008). Given how rarely the initial choice in the study by Balewski et al. (as indicated by the first saccade) was overturned through deliberation, maybe the more interesting question to ask is whether the result of "deliberation" is, in fact, deliberate.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Balewski, Z.Z., Knudsen, E.B., and Wallis, J.D. (2022). Fast and slow contributions to decision-making in corticostriatal circuits. Neuron *110*, 2170–2182. https://doi.org/10.1016/j.neuron.2022.04.005.

Bigelow, H.J. (1850). Art. I.—Dr. Harlow's case of recovery from the passage of an iron bar through the head. Am. J. Medical Sci. *16*, 13–22. https://doi.org/10.1097/00000441-185016390-00001.

Kahneman, D. (2011). Thinking, Fast and Slow (Macmillan).

Lau, B., and Glimcher, P.W. (2007). Action and outcome encoding in the primate caudate nucleus. J. Neurosci. *27*, 14502–14514. https://doi.org/10.1523/jneurosci.3060-07.2007.

Libet, B., Gleason, C.A., Wright, E.W., and Pearl, D.K. (1983). Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): The unconscious initiation of a freely voluntary act. Brain *106*, 623–642. https://doi.org/10.1093/brain/106.3.623.

Soon, C.S., Brass, M., Heinze, H.-J., and Haynes, J.-D. (2008). Unconscious determinants of free decisions in the human brain. Nat. Neurosci. *11*, 543–545. https://doi.org/10.1038/nn.2112.

Wood, S.M.W., and Bechara, A. (2014). The neuroscience of dual (and triple) systems in decision making. In The Neuroscience of Risky Decision Making (American Psychological Association), pp. 177–202. https://doi.org/10.1037/14322-008.

Zhou, J., Gardner, M.P., and Schoenbaum, G. (2021). Is the core function of orbitofrontal cortex to signal values or make predictions? Curr. Opin. Behav. Sci. *41*, 1–9. https://doi.org/10.1016/j.cobeha.2021.02.011.

A stare like yours: Naturalistic social gaze interactions reveal robust neuronal representations

Raymundo Báez-Mendoza[1,*] and Ziv M. Williams[1,2,3]
[1]Department of Neurosurgery, Massachusetts General Hospital, Harvard Medical School, Boston, MA 02114, USA
[2]Harvard-MIT Division of Health Sciences and Technology, Boston, MA 02115, USA
[3]Program in Neuroscience, Harvard Medical School, Boston, MA 02115, USA
*Correspondence: rbaez-mendoza@mgh.harvard.edu
https://doi.org/10.1016/j.neuron.2022.06.007

In this issue of *Neuron*, Dal Monte, Fan, and colleagues (Dal Monte et al., 2022) show that rhesus monkeys have a widely distributed and robust neuronal representation of social gaze: looking at others and where others are looking.

Consider these everyday life situations. While playing cards with a friend, their poker face does not reveal their emotions, yet their eye movements reveal what they intend to do. A crowd of people outside of a skyscraper stare at the top of the building. People sitting in a café, chatting, and staring at passersby.

In all these situations, we acquire information about others and our environment by following the gaze of others. Real-life social gaze interactions are fundamental to almost all aspects of primate and human behavior, and, therefore, studying their neuronal underpinnings is essential to our understanding of social behavior. Living in large social groups forces us to decode and value social signals in order to interact effectively with others. In primates, one of the most informative sources of social signals is the others' gaze.

Most neurophysiological studies of gaze perception have, rightly, focused on the temporal lobe cortex, where clusters of neurons selectively respond to faces and their features, including face orientation and viewing direction (Tsao and Livingstone, 2008). Other studies also localized so-called face patches in the prefrontal cortex, including gaze direction (Morin et al., 2015). Neurons in the amygdala, on the other hand, encode mutual gaze (Gothard, 2020; Pryluk et al., 2020). Yet, it is not clear whether and how different prefrontal cortical areas and the amygdala, which comprise part of the social attention network, encode others' gaze or what precise computations they may perform.

The neurophysiological correlates of social gaze have been typically studied with well-controlled visual stimuli shown on monitors. Yet, there is a growing recognition that social interactions are not necessarily mediated by a screen. Further, numerous studies across multiple species have highlighted the importance of studying neural activity during real-world face-to-face social interactions (Báez-Mendoza et al., 2021; Redcay and Schilbach, 2019). In the main paradigm of Dal Monte, Fan, and colleagues in this issue of *Neuron*, they had two rhesus monkeys face each other for a limited amount of time while their eye positions and the neuronal activity from one of them were recorded (Dal Monte et al., 2022). During this time, the animals could freely gaze at each other or at objects placed lateral to the other conspecific's face. The researchers then recorded single neuronal activity from three different prefrontal brain areas and the amygdala during task performance. They then tested for the presence of three gaze-sensitive signatures in the activity of these neurons: (1) discriminability between looking at an object versus at the conspecific; (2) parametric modulation of the gaze of both animals, i.e., the direction and distance of their gaze relative to the center; and (3) modulation during mutual gaze, i.e., when they stared at each other. Together, using this powerful tool to investigate the neuronal basis of social interactions and gaze, the authors found single neurons in all brain regions that responded with these signatures, and the results suggest fairly similar responses to social gaze across these different brain regions.

The findings from this study emphasize the importance of real, face-to-face interactions in the neuronal responses to gaze behavior. The authors previously showed that in this task (Dal Monte et al., 2016), monkeys behaved differentially when interacting with images of monkeys than they did with live monkeys. Consistent with the value of observing others, monkeys looked more often and for longer at the others than the object that was to the side. Neurons in all recorded regions showed selectivity for looking at others. More notably, the neurons also displayed parametric modulation based on the other's gaze direction. Further, when we look into each other's eyes, one individual begins the interaction while the other follows. In this task, when monkeys stared at each other, i.e., they had mutual eye contact, neuronal signals differentiated between following and being followed, and these were represented by distinct neurons. Further, more neurons responded to mutual gazing than when the monkeys stared at the other. These findings may underscore gaze following, whereby information is gleaned by following the direction of the other's gaze, like in the real-world situations described above.

Taken together, this extraordinary paper by Chang and colleagues provides an unprecedented look into the widespread network of brain areas involved in naturalistic social gaze. The results suggest that, across this network, there is a "shared code" to represent the social gaze with some important nuances. Overall, this study highlights a new tool by which to investigate the neuronal basis of social interactions and naturalistic social gaze. Further, by recording from multiple areas in the primate brain rather than one, this work provides fundamental new insights into the network of brain areas involved in social behavior.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Báez-Mendoza, R., Mastrobattista, E.P., Wang, A.J., and Williams, Z.M. (2021). Social agent identity cells in the prefrontal cortex of interacting groups of primates. Science *374*, eabb4149. https://doi.org/10.1126/science.abb4149.

Dal Monte, O., Fan, S., Fagan, N.A., Chu, C.-C.J., Zhou, M.B., Putnam, P.T., Nair, A.R., and Chang, S.W.C. (2022). Widespread Implementations of interactive social gaze neurons in the primate prefrontal-amygdala networks. Neuron *110*, 2183–2197. https://doi.org/10.1016/j.neuron.2022.04.013.

Dal Monte, O., Piva, M., Morris, J.A., and Chang, S.W.C. (2016). Live interaction distinctively shapes social gaze dynamics in rhesus macaques. J. Neurophysiol. *116*, 1626–1643. https://doi.org/10.1152/jn.00442.2016.

Gothard, K.M. (2020). Multidimensional processing in the amygdala. Nat. Rev. Neurosci. *21*, 565–575. https://doi.org/10.1038/s41583-020-0350-y.

Morin, E.L., Hadj-Bouziane, F., Stokes, M., Ungerleider, L.G., and Bell, A.H. (2015). Hierarchical encoding of social cues in primate inferior temporal cortex. Cereb. Cortex *25*, 3036–3045. https://doi.org/10.1093/cercor/bhu099.

Pryluk, R., Shohat, Y., Morozov, A., Friedman, D., Taub, A.H., and Paz, R. (2020). Shared yet dissociable neural codes across eye gaze, valence and expectation. Nature *586*, 95–100. https://doi.org/10.1038/s41586-020-2740-8.

Redcay, E., and Schilbach, L. (2019). Using second-person neuroscience to elucidate the mechanisms of social interaction. Nat. Rev. Neurosci. *20*, 495–505. https://doi.org/10.1038/s41583-019-0179-4.

Tsao, D.Y., and Livingstone, M.S. (2008). Mechanisms of face perception. Annu. Rev. Neurosci. *31*, 411–437. https://doi.org/10.1146/annurev.neuro.30.051606.094238.