tractable [5,11], this approach can now provide powerful solutions to broadening scientific investigation. To fully realize its potential, a next challenge will be to creatively adjust these methods for use across the different subdisciplines of the cognitive sciences (e.g., psychology, neuroscience, linguistics, artificial intelligence) and in different human societies. To aid in this challenge, technological advances could support the collection of data across multiple and distant sites. For example, wearable non-intrusive devices designed for different ecological niches could objectively measure a variety of behaviors such as social proximity, hand and arm gestures, and eye movements. Widening scientific lenses can also be achieved by importing knowledge from neighboring scientific disciplines such as anthropology, biology, linguistics, physics, engineering, and computer science. For example, integrating behavioral ecology into the study of facial expressions has diversified concepts of their function [12].

Conclusions: Discovering New Lands

Decades of evidence and appeals from scholars in several subdisciplines of the cognitive sciences demonstrate that the psychological science community can no longer overlook the inextricable role of culture in shaping human perception, thought, and action. To understand and represent the diversity of human psychology, the discipline must undergo a significant conceptual and cultural shift to relax the constraints of a theory-driven approach, and achieve its ultimate goal as a scientific discipline – a deep understanding of human behavior from universal laws to cultural complexity.

Acknowledgments

This work was supported with funding from the Economic and Social Research Council and Medical Research Council (ESRC/MRC-060-25-0010), Economic and Social Research Council (ES/K001973/1), and British Academy (SG113332) to R.E.J., and from the National Institutes of Health (NIH; 1R01MH112566-01) to T.W.

[1]Institute of Neuroscience and Psychology, University of Glasgow, Glasgow, UK
[2]School of Psychology, University of Glasgow, Glasgow, UK
[3]School of Applied Social Sciences, De Montfort University, Leicester, UK
[4]Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

*Correspondence:
rachael.jack@glasgow.ac.uk (R.E. Jack).

https://doi.org/10.1016/j.tics.2017.10.002

References

1. Schyns, P.G. (1991) A modular neural network model of concept acquisition. *Cogn. Sci.* 15, 461–508
2. Danziger, K. (2006) Universalism and indigenization in the history of modern psychology. In *Internationalizing the History of Psychology* (Brock, A.C., ed.), pp. 208–225, New York University Press
3. Henrich, J. *et al.* (2010) The weirdest people in the world? *Behav. Brain Sci.* 33, 61–83
4. Medin, D. *et al.* (2017) Systems of (non-) diversity. *Nat. Hum. Behav.* 1, 0088
5. Jack, R. *et al.* (2016) Four not six: revealing culturally common facial expressions of emotion. *J. Exp. Psychol. Gen.* 145, 708–730
6. Sievers, B. *et al.* (2013) Music and movement share a dynamic structure that supports universal expressions of emotion. *Proc. Natl. Acad. Sci. U. S. A.* 110, 70–75
7. Majid, A. and Burenhult, N. (2014) Odors are expressible in language, as long as you speak the right language. *Cognition* 130, 266–270
8. Crivelli, C. *et al.* (2017) Recognizing spontaneous facial expressions of emotion in a small-scale society of Papua New Guinea. *Emotion* 17, 337–347
9. Crivelli, C. *et al.* (2016) A multidisciplinary approach to research in small-scale societies: studying emotions and facial expressions in the field. *Front. Psychol.* 7, 1073
10. Yu, H. *et al.* (2012) Perception-driven facial expression synthesis. *Comput. Graph.* 36, 152–162
11. Hirschberg, J. and Manning, C.D. (2015) Advances in natural language processing. *Science* 349, 261–266
12. Fridlund, A.J. (1994) *Human Facial Expression: An Evolutionary View*, Academic Press
13. Ekman, P. (1972) Universals and cultural differences in facial expressions of emotion. In *Nebraska Symposium on Motivation* (Cole, J., ed.), pp. 207–282, University of Nebraska Press
14. Jack, R.E. (2013) Culture and facial expressions of emotion. *Vis. Cogn.* 21, 1248–1286
15. Nelson, N.L. and Russell, J.A. (2013) Universality revisited. *Emot. Rev.* 5, 8–15

Spotlight

Single-Neuron Correlates of Awareness during Attentional Blinks

Zhongzheng Fu[1] and Ueli Rutishauser[2,3,4,*]

A recent single-neuron study revealed an anatomical anterior-to-posterior gradient of awareness-related responses by 'concept neurons' in the human medial temporal lobe (MTL). Delayed and weaker responses were indicative of the failure of a stimulus to reach awareness, suggesting that reliable fast responses are a critical aspect of the neural mechanisms of consciousness.

Figure I. (A) Data-Driven Modeling of Dynamic Facial Expressions of Emotion. On each experimental trial a dynamic facial expression generator [10] creates a random facial animation by randomly sub-sampling a set of individual face movements called Action Units (AUs) – here, Upper Lid Raiser (AU5), Nose Wrinkler (AU9), and Upper Lip Raiser (AU10) – and by assigning a random movement to each AU using several temporal parameters (see labels illustrating the red curve). The randomly activated AUs are then combined to produce a facial animation (see bottom row of faces) which the cultural observer categorizes by emotion and rates by intensity (here, 'disgust' and 'medium' intensity) if it matches their prior knowledge of that facial expression. Otherwise, they select 'other'. Statistical tools can then be used to build a relationship between the dynamic AU patterns presented on each trial and the observer's responses to deliver a precise mathematical model of the face movement patterns that communicate emotions to individuals within a society. These models can then be precisely analyzed to reveal the cross-cultural facial expression patterns and their specific accents. (B) Cross-cultural facial expression patterns and specific accents. Color-coded face maps (top row) show four core facial expression patterns associated with 60+ emotions across two distinct societies (Western and East Asian). The bottom row of faces shows the specific accents that modify each core expressive pattern to create different facial expressions such as 'contempt', 'shame', 'ecstatic', and 'fury'.

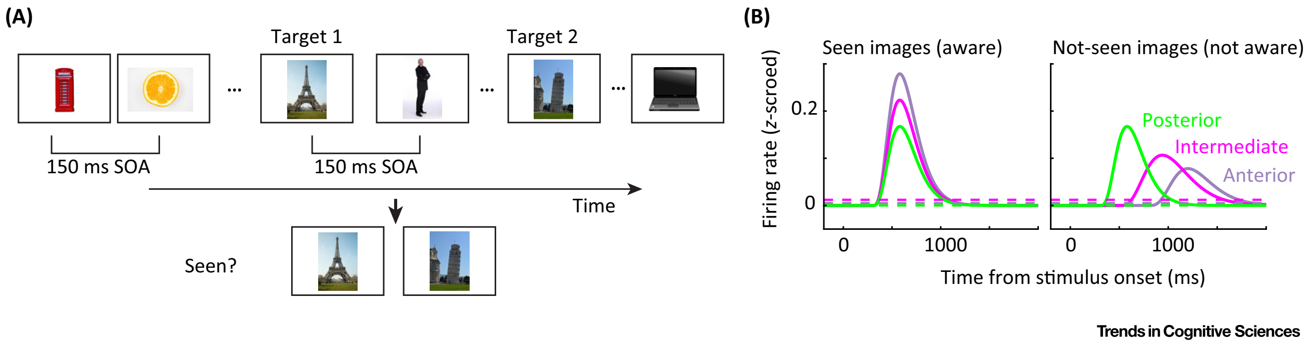

Figure 1. Experimental Setup and Principal Observation of Reber *et al*. [1]. (A) Illustration of the task. Two target images were embedded in a sequence of stimuli shown with a stimulus onset asynchrony (SOA) of 150 ms. After each trial, subjects indicated for each target whether they had seen it or not (bottom). (B) Summary of the principal observation. The response of concept cells to their preferred stimulus (straight lines) was reduced in amplitude and occurred later when a stimulus was not seen. This difference between seen and unseen images was most pronounced in the anterior medial temporal lobe (MTL) (i.e., the amygdala). The neurons did not modulate their firing rate in response to non-preferred stimuli (broken lines).

Although a vast amount of information is captured and processed by the nervous system, only a small subset of this information is consciously perceived. Many experiments have revealed this cognitive bottleneck, but the neural processes that elevate a processed sensory stimulus to a state of conscious perception remain largely unknown. Developing a better understanding of this process is critical to resolving one of the biggest remaining mysteries in neuroscience: the neural mechanisms of consciousness.

Recently, Reber and colleagues [1] used ‘concept neurons’ to investigate the neural mechanisms underlying conscious perception. A concept neuron is a visually responsive neuron in the human MTL that is tuned to a single specific concept [2]. For instance, some concept neurons increase their activity specifically to images that contain Jennifer Aniston [2]. In their study, Reber *et al*. [1] explored whether concept cells responded differently to the same stimulus when it was consciously perceived versus when it was not, with the goal of determining whether concept cells in different parts of the MTL would differentially correlate with conscious perception.

The authors first identified images that elicited selective responses from different concept cells. They then embedded two of these images within a stream of distractors and asked participants to determine whether the sequence of images contained the targets (Figure 1A). Previous work has established that during this ‘rapid serial visual presentation’ task (RSVP), a target image that follows within about 300 ms of another target image tends to fail to reach awareness. This phenomenon, known as ‘attentional blink’, possibly reflects limits on how fast attention can switch between targets. The key question was how concept cells would respond during attentional blinks.

Prior work has shown that the activity of MTL concept cells remains unchanged when a target is not consciously perceived [3,4]. By contrast, Reber *et al*. [1] have found that neurons in the anterior parts of the MTL (the amygdala and part of the hippocampus) still increased their firing rates when presented with unseen targets, albeit with less intensity and much later onset. Neurons recorded in the posterior MTL, however, responded in the same way to seen and unseen targets. These differential response patterns reveal an anatomical gradient within the MTL (Figure 1B).

These findings raise important questions. First, what explains the difference between the new study [1] and prior work [3,4]? Previous experiments relied on the disruption of low-level sensory processes using backward masking or binocular rivalry. Consequently, visual information about unseen stimuli is likely to have never reached the MTL, explaining why responses to unseen stimuli were not observed in these paradigms. By contrast, in [1] stimuli failed to reach awareness due to the dynamic limits of top-down attention instead of insufficient visual processing, as is evident from the response of posterior MTL concept cells. Interestingly, unperceived stimuli triggered a less intense but more variable response from the anterior MTL concept cells, suggesting that the timing of spikes is important for conscious perception.

Second, why are responses in the MTL, an area classically known for its role in memory, correlated with conscious perception? One possible explanation is that the RSVP task depends on working memory. Previous work has shown that concept cells within the MTL support working memory through persistent activity [5]. Interestingly, previous work has also shown that when stimuli are presented in succession with sufficient time for conscious perception (200 ms), ongoing activity of some concept cells is terminated by the onset of the next stimulus

[6]. This suggests that target images may not have been perceived because of a failure to initiate and terminate persistent activity in a timely manner. A second possibility is that persistent activity itself has a role in visual awareness, a hypothesis that posits that persistent activity supports the large-scale distributed synchronization necessary to provide the 'ignition' that lifts a stimulus into consciousness [7].

The results of Reber *et al*. [1] also speak to other aspects of the neural mechanisms of consciousness. The finding that the activity of anterior MTL (i.e. amygdala) neurons indicates visual awareness most reliably adds to the growing literature on the role of the amygdala in awareness [8]. A related proposal is that the amygdala's role is to enhance the likelihood that stimuli with affective value reach awareness. However, this hypothesis rests largely on work with fearful faces, whereas the stimuli used by Reber *et al*. [1] were not aversive. In addition, the findings of Reber *et al*. [1] do not support the view that a fast subcortical pathway enables amygdala neurons to rapidly respond to visual stimuli even when they are not consciously perceived [8]. Instead, the response to unperceived stimuli was delayed and weaker. A critical future experiment will be to repeat the RSVP experiment with emotional faces. Amygdala neurons differentiate between facial emotions [9], making it possible to test directly whether amygdala neurons signal emotions of unseen faces during the attentional blink.

Oscillations are thought to be critical for consciousness because they coordinate neural activity across large numbers of neurons. The study of concept cells in the MTL has already provided evidence for this proposal. Stimulus-triggered theta power in the MTL is indicative of awareness and the activity of concept cells is coordinated by these theta oscillations [10]. Together with Reber *et al*. [1], this suggests that theta oscillations and the resulting coordination of concept-cell persistent activity might be a mechanism contributing to visual awareness. The robust but delayed responses to unseen stimuli during the RSVP task [1], which were absent from previous paradigms, might make it possible to examine this question directly from the perspective of spike-field coherence.

In summary, Reber *et al*. [1] reveal an anatomical anterior-to-posterior gradient of awareness-related response within the MTL and suggests that concept cells in the amygdala and hippocampus might support conscious perception through persistent activity. This is both a critical new insight into the neural mechanisms of consciousness and a demonstration of the powerful insights enabled by single-neuron recordings in humans.

[1]Control and Dynamical Systems Program, Department of Computing + Mathematical Sciences, California Institute of Technology, Pasadena, CA, USA
[2]Department of Neurosurgery, Cedars-Sinai Medical Center, Los Angeles, CA, USA
[3]Center for Neural Science and Medicine, Cedars-Sinai Medical Center, Los Angeles, CA, USA
[4]Division of Biology and Biological Engineering, California Institute of Technology, Pasadena, CA, USA

*Correspondence:
ueli.rutishauser@cshs.org (U. Rutishauser).
https://doi.org/10.1016/j.tics.2017.10.005

References

1. Reber, T.P. *et al.* (2017) Single-neuron correlates of conscious perception in the human medial temporal lobe. *Curr. Biol.* 27, 2991–2998 e2
2. Quiroga, R.Q. *et al.* (2005) Invariant visual representation by single neurons in the human brain. *Nature* 435, 1102–1107
3. Quiroga, R.Q. *et al.* (2008) Human single-neuron responses at the threshold of conscious recognition. *Proc. Natl. Acad. Sci. U. S. A.* 105, 3599–3604
4. Kreiman, G. *et al.* (2002) Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proc. Natl. Acad. Sci. U. S. A.* 99, 8378–8383
5. Kaminski, J. *et al.* (2017) Persistently active neurons in human medial frontal and medial temporal lobe support working memory. *Nat. Neurosci.* 20, 590–601
6. Kornblith, S. *et al.* (2017) Persistent single-neuron activity during working memory in the human medial temporal lobe. *Curr. Biol.* 27, 1026–1032
7. Dehaene, S. *et al.* (2014) Toward a computational theory of conscious processing. *Curr. Opin. Neurobiol.* 25, 76–84
8. Adolphs, R. (2008) Fear, faces, and the human amygdala. *Curr. Opin. Neurobiol.* 18, 166–172
9. Wang, S. *et al.* (2014) Neurons in the human amygdala selective for perceived emotion. *Proc. Natl. Acad. Sci. U. S. A.* 111, E3110–E3119
10. Rey, H.G. *et al.* (2014) Timing of single-neuron and local field potential responses in the human medial temporal lobe. *Curr. Biol.* 24, 299–304