6. Müller, M., and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. Proc. Natl. Acad. Sci. USA *85*, 5287–5290.

7. Ofstad, T.A., Zuker, C.S., and Reiser, M.B. (2011). Visual place learning in *Drosophila melanogaster*. Nature *474*, 204–207.

8. van Breugel, F., and Dickinson, M.H. (2014). Plume-tracking behavior of flying *Drosophila* emerges from a set of distinct sensory-motor reflexes. Curr. Biol. *24*, 274–286.

9. Wittlinger, M., Wehner, R., and Wolf, H. (2006). The ant odometer: stepping on stilts and stumps. Science *312*, 1965–1967.

10. Pfeffer, S.E., and Wittlinger, M. (2016). Optic flow odometry operates independently of stride integration in carried ants. Science *353*, 1155–1157.

11. McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., and Moser, M.-B. (2006). Path integration and the neural basis of the 'cognitive map'. Nat. Rev. Neurosci. *7*, 663–678.

12. Seelig, J.D., and Jayaraman, V. (2015). Neural dynamics for landmark orientation and angular path integration. Nature *521*, 186–191.

13. Green, J., Adachi, A., Shah, K.K., Hirokawa, J.D., Magani, P.S., and Maimon, G. (2017). A neural circuit architecture for angular integration in *Drosophila*. Nature *546*, 101–106.

14. Turner-Evans, D., Wegener, S., Rouault, H., Franconville, R., Wolff, T., Seelig, J.D., Druckmann, S., and Jayaraman, V. (2017). Angular velocity integration in a fly heading circuit. eLife *6*, e23496.

15. Liu, G., Seiler, H., Wen, A., Zars, T., Ito, K., Wolf, R., Heisenberg, M., and Liu, L. (2006). Distinct memory traces for two visual features in the *Drosophila* brain. Nature *439*, 551–556.

16. Homberg, U., Heinze, S., Pfeiffer, K., Kinoshita, M., and el Jundi, B. (2011). Central neural coding of sky polarization in insects. Phil. Trans. R. Soc. Lond. B *366*, 680–687.

Neuroscience: Decision, Insight and Intention

Benjamin Y. Hayden[1,*] and Patrick Haggard[2]
[1]Brain and Cognitive Sciences, Center for Visual Science, and Center for the Origins of Cognition, University of Rochester, Rochester, NY 14627, USA
[2]Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK
*Correspondence: benhayden@gmail.com
http://dx.doi.org/10.1016/j.cub.2017.06.065

A new study of perceptual decision making in which subjects were asked to report, after indicating their choice, precisely when they felt they had made a decision, supports the idea that conscious awareness occurs when evidence has accumulated beyond some threshold.

In 1983, Benjamin Libet [1] published a study that quickly became a centerpiece of philosophical and pub debates on free will. Libet examined the properties of the *bereitschaftspotential* (German for 'readiness potential'), a slight deflection in the brain's electroencephalographic signal that can be observed prior to deliberate action. The signal, which is thought to emanate from the premotor cortex, slowly grows stronger over time as the action becomes more imminent. But, in its weaker form, it stretches back surprisingly far in time. Libet wanted to know whether it went back far enough that it actually preceded the conscious urge to move. If it did, that would imply the conscious urge occurred as a consequence of the preparation, perhaps as a side effect of the actual process that initiated the decision — after the train had left the station so to speak.

Since Libet's original study [1], several others have confirmed and extended his results (for example [2,3]; reviewed in [4]). More broadly, the use of self-reporting to study conscious awareness is a mainstay of neuroscience (for example [5]). The key trick has been to precisely measure the time at which subjects felt the conscious urge to move. Libet devised a small clock-like function on his oscilloscope that swept in a circle; subjects watched and when they reported the urge to move made a mental note of the position of the rotating dot. Assuming people could take a mental snapshot of the clock face at the moment they consciously decided, the plan provided a good measure of the time of the conscious urge.

As reported by Kang *et al.* [6] in this issue of *Current Biology*, our reports of the time at which we become consciously aware may indeed be accurate. The authors examined the report times of subjects performing a dot motion discrimination task and found that they obey several lawful properties associated with sequential sampling models.

Can We Accurately Measure Our Conscious Awareness of the Urge to Move?

Libet's method of measuring the time of conscious urges was crucial to his experiment. But, since the original study, the question of whether it accurately measures the time of the conscious urge has attracted a great deal of scrutiny (for example [7]). The question of what leads to our awareness of our internal volition has not been resolved. Kang *et al.* [6] believe that conscious awareness is the result of some subconscious process that increases in intensity and, as it rises, may pass some internal threshold; then, when it does so, it pops above the clouds and into conscious awareness. In other words, they propose that consciousness works very much the same way that perceptual decisions work.

This new work [6] takes as its foundation an ostensibly unrelated, but also very influential, set of studies showing that when viewing a field of moving dots, the perception of coherent motion obeys certain laws of sequential sampling [8]. Specialized neurons in the middle temporal (MT) brain region monitor motion in small patches of space, albeit in a noisy way, and these monitoring signals are integrated into a decision variable. In monkeys, this variable can be measured in the responses of neurons in one particular brain region, and it obeys several lawful rules. In particular, it rises to a specific threshold and, when that threshold is achieved, a decision to act is initiated. These same sequential sampling principles apply to other forms of decision-making as well, including stopping decisions, economic decisions and abstract strategic decisions [9–12].

The key thing to know about this process, known as bounded evidence accumulation, is that its signature is a close correspondence between threshold crossing time and decision accuracy. Thus, the key result of the Kang *et al.* [6] study is that easier trials (those with more coherent motion) showed more rapid perceptual reports; a bounded drift-diffusion model predicted the timing of the reports.

In a second experiment, Kang *et al.* [6] allowed subjects to indicate the time at which they experienced the percept. This allowed them to know the time at which the decision was made. It also allowed them to calibrate the first experiment and answer a question that has heretofore puzzled philosophers — can we place any trust in the subjective estimate of conscious awareness?

Implications for Theories of Decision-making

Systems neuroscientists are, ostensibly, philosophical materialists and monists. That is, we believe that, as inscrutable as consciousness seems, it is nothing more than a product of prosaic neural circuit principles. But accepting this idea in theory doesn't make it any easier to intuitively get what consciousness is. As a consequence, consciousness is often a bit mystical and a bit separated from the rest of cognitive neuroscience.

This new study [6] offers the possibility to see, through a glass darkly, how consciousness might be eventually reduced to simpler processes. Specifically, it suggests that our mind contains a large and heterogeneous pool of mostly unconscious notions that wax and wane with endogenous and exogenous demands; sometimes, when some coherent thoughts wax enough, they cross some threshold and 'pierce', to use the authors' term, the veil of consciousness and enter conscious awareness.

In the case of dot motion, these notions are guesses about the direction of motion. After all, neurons in MT are noisy and plentiful — at any moment, a large number are signaling every possible direction of motion. The only time we perceive the motion consciously though is when enough are making a coherent signal (that is, are in agreement) that their collective activity passes some sort of threshold. The analogy to other processes is straightforward; indeed, the ideas from the dot motion task have already been applied to other sensory domains, like form vision and auditory perception, as well as to economic decisions, executive control, and motor plans. It should be difficult to imagine it would apply to conscious awareness as well.

This view is appealing because it allows a direct link to a body of literature on the neuroscience of perceptual decision-making. We have a good understanding of how activity of single neurons in areas MT and LIP (lateral intraparietal cortex) corresponds to these constituent notions; we have a sense of how they can cohere, and how both exogenous and endogenous factors regulate that process [8]. And we have some understanding of how that threshold is implemented. Moreover, this framework has been influential in neuroscience, and applies beyond the scope of perception, to action planning, and even abstract things like strategic adjustment.

This reductive view offers a solution to an important problem in consciousness: how are the contents of consciousness selected? In a conventional view, we need a central executive, a super-conscious homunculus, to scan the possible contents of consciousness and choose one, and somehow shove the chosen one forward. In the reductive view, on the other hand, achieving consciousness is a bottom-up process; it results from coordinated signaling with no central executive. Such emergent, bottom-up controlled systems are not necessarily intuitive, but they apply to many biological systems, and may apply to executive functions in the human brain [13]. And they may apply to consciousness as well: for example, Dennett [14] has proposed that conscious awareness may work the way (the emergent process of) becoming famous works: no agent decides who will become famous, it is a by-product of the interactions that constitute human society.

Implications for Consciousness

The new paper of Kang *et al.* [6] also prompts some new thinking about the nature of consciousness itself. Recent scientific studies of perceptual consciousness triangulate around three separate elements of conscious processing. That is, the main differences between theories of consciousness lie in the weight given to one of these aspects relative to the other two. The three elements can be summarised, rather alliteratively, as Input, Intent, and Insight.

Input refers to the raw consciousness of sentient experience, typically triggered by a sensory input. It corresponds to the philosophical concept of qualia, and typically forms a key content of conscious experience. In the new study [6], the input element refers to the perceptual content that the dots are moving in one direction, rather than another. The neural substrate for this content is thought to be area MT.

Intent in the context of perceptual decision-making means being 'on task'. It is what an animal or a person is engaged in processing at a particular time, and it determines the focus of their attention. In this study [6], participants are asked to perceive motion direction: they are looking at the screen, attending to the dots, and ready to respond. Key mechanisms for the role of intent in determining conscious content are the recurrent, top-down projections from frontal and associative areas into primary sensory cortices [15]. These recurrent projections are thought to play a major role in directing and coordinating processing of input information, so that afferent information is selected [16], or even constructed [17] for current purposes, rather than simply passively received.

Finally, the *insight* aspect of consciousness refers to the 'aha' moment, typically associated with realising the solution to a problem, or grasping the meaning of an event. This has been linked to a sudden 'ignition' of a global workspace, characterised by an increased connectivity and long-range interaction between multiple cortical areas [18]. Interestingly, the global workspace tradition of studying consciousness has often focused on tasks involving mental operations on stimuli that are explicitly semantic or symbolic (for example, words and numbers). The task in the present study [6] seems simpler, and is perceptual rather than symbolic.

Theories of perceptual consciousness can be broadly classified according to the relative importance they accord to phenomenality *versus* information processing. Phenomenal accounts will typically place a strong emphasis on inputs while downplaying insight. Accounts that treat consciousness as the subjective upshot of current cognitive operations, such as working memory accounts, typically downplay inputs and emphasise insight [19]. This dimension of variation among consciousness theories is worth spelling out explicitly, because the present study involves a quite distinctive, even radical, reorganisation of the traditional contrast between input and insight accounts. Strikingly, the new paper [6] focusses on input consciousness, in a simple perceptual decision-making task, yet the experience that it produces has the subjective character and the formal computational properties of insight. Participants need only figure out the net direction of dot motion. Multiple occipito-parietal areas have specific detector neurons that appear to be specialised for this computation.

Previous work by the same group showed that neurons in monkey area LIP perform a simple evidence-based computation which is sufficient (though perhaps not necessary) to make the perceptual decision. What monkeys *experience* in these tasks is much harder to assess, because they cannot tell us directly — though they do seem at least to experience that a particular perceptual decision is harder or easier [20]. The Kang *et al.* [6] paper shows that the process of evidence accumulation within a delimited input-processing module can also lead to a distinctive, reportable experience of decision, which the authors term an 'aha moment'.

This seems remarkably like insight. However, the key features of global connectivity, problem solving, symbol manipulation, linguistic meaning, and 'higher' cognition all appear absent here. Instead, the present paper suggests that accumulation of input evidence, perhaps by a single encapsulated sensory-processing module, may be sufficient for the insight element of perceptual consciousness. The Kang *et al.* [6] paper thus seems to break the currently dominant link between insight and a symbolic, problem-solving aspect of consciousness.

If so, the link between insight-like features of consciousness and massive cortical interconnection may be overstated. Insight may be more like a threshold of input evidence than like an ignition of symbolic thought. The paper ends with an intriguing, perhaps bold claim that the problems of consciousness may not, in fact, be as intractable and scientifically elusive as is sometimes claimed. By suggesting that insight-like features of consciousness can be clearly linked to input-like features, this paper calls into question some of the stressed insight-based global workspace theories. Specifically, the Kang *et al.* [6] paper suggests that cumulation of input evidence may be sufficient for an 'aha moment' phenomenon.

Conclusion

Kang *et al.* [6] did not particularly set out to investigate the intent aspect of consciousness, and this remains an enigma. It remains unclear how and why people, and monkeys, are able, at will, to latch their cognitive resources onto a set of moving dots. Their new study takes a strongly bottom-up approach: this is a simplifying and justifiable decision. The exceptional feature of consciousness may be our ability to deploy cognitive resources to what we currently want to focus on, rather than our ability to achieve insight by doing so. We began this commentary with Libet's investigations of willed action. Perhaps the remarkable feature of attention and will is not the fact that willing an action can sometimes involve an 'aha moment', but rather the distinctive human capacity to voluntarily switch engagement between different tasks, and different action goals, from one moment to the next.

REFERENCES

1. 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.
2. 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.
3. Brass, M., and Haggard, P. (2008). The what, when, whether model of intentional action. Neuroscientist *14*, 319–325.
4. Haggard, P. (2008). Human volition: towards a neuroscience of will. Nat. Rev. Neurosci. *9*, 934–946.
5. Leopold, D.A., and Logothetis, N.K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. Nature *379*, 549–553.
6. Kang, Y.H.R., Petzschner, F.H., Wolpert, D.M., and Shadlen, M.N. (2017). Piercing of consciousness as a threshold crossing operation. Curr. Biol. *27*, 2285–2295.
7. Dennett, D.C., and Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. Behav. Brain Sci. *15*, 183–247.
8. Gold, J., and Shadlen, M. (2007). The neural basis of decision making. Annu. Rev. Neurosci. *30*, 535–574.
9. Pisauro, M.A., Fouragnan, E., Retzler, C., and Philiastides, M.G. (2017). Neural correlates of evidence accumulation during value-based decisions revealed via simultaneous EEG-fMRI. Nat. Commun. *8*, 15808.
10. Heilbronner, S.R., and Hayden, B.Y. (2016). Dorsal anterior cingulate cortex: a bottom-up view. Annu. Rev. Neurosci. *39*, 149–170.
11. Logan, G.D., Yamaguchi, M., Schall, J.D., and Palmeri, T.J. (2015). Inhibitory control in mind and brain 2.0: Blocked-input models of saccadic countermanding. Psychol. Rev. *122*, 115–147.
12. Hayden, B.Y., Smith, D.V., and Platt, M.L. (2010). Cognitive control signals in posterior cingulate cortex. Front. Hum. Neurosci. *4*, 223.
13. Eisenreich, B.R., Akaishi, R., and Hayden, B.Y. (2017). Control without controllers: toward a distributed neuroscience of executive control. J. Cogn. Neurosci. http://dx.doi.org/10.1162/jcon_a_01139.
14. Dennett, D. (2001). Are we explaining consciousness yet? Cognition *79*, 221–237.

15. Bressler, S.L., Tang, W., Sylvester, C.M., Shulman, G.L., and Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. J. Neurosci. *28*, 10056–10061.

16. Vandenbroucke, A.R.E., Fahrenfort, J.J., Meuwese, J.D.I., Scholte, H.S., and Lamme, V.A.F. (2016). Prior knowledge about objects determines neural color representation in human visual cortex. Cereb. Cortex *26*, 1401–1408.

17. Wokke, M.E., Vandenbroucke, A.R.E., Scholte, H.S., and Lamme, V.A.F. (2013). Confuse your illusion. Psychol. Sci. *24*, 63–71.

18. Dehaene, S., and Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. Neuron *70*, 200–227.

19. Jack, A.I., and Shallice, T. (2001). Introspective physicalism as an approach to the science of consciousness. Cognition *79*, 161–196.

20. Kiani, R., and Shadlen, M.N. (2009). Representation of confidence associated with a decision by neurons in the parietal cortex. Science *324*, 759–764.

Communication: Animal Steps on the Road to Syntax?

Andrew F. Russell[1] and Simon W. Townsend[2,3]
[1]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE, UK
[2]Department of Psychology, University of Warwick, University Road, Coventry CV4 7AL, UK
[3]Department of Comparative Linguistics, University of Zurich, Plattenstrasse 54, 8032 Zurich, Switzerland
Correspondence: a.russell@exeter.ac.uk (A.F.R.), simonwilliam.townsend@uzh.ch (S.W.T.)
http://dx.doi.org/10.1016/j.cub.2017.06.066

From tool use to teaching, proto-forms of ‘human traits’ are being discovered in animals. But what of language? New evidence suggests that a garden bird has hopped on the long road to syntax, an integral component of language.

Of all the traits considered to be uniquely human, language is amongst the most defining. No other extant animal species naturally uses language, and language has likely been pivotal to humanity’s current success [1]. Understanding the emergence of humanity thus, in part, requires an understanding of the emergence of language. A prevailing hypothesis is that the core components of language evolved uniquely during hominin evolution [2]. But as reported by Suzuki *et al.* [3] in this issue of *Current Biology*, new work on the Japanese tit (*Parus minor*), a common garden bird of eastern Asia, provides compelling evidence that animals can compose meaningful sequences by joining specific calls in rule-guided combinations — a requisite of compositional syntax [4].

Human language is characterised by the ability to combine sounds generatively [4]. First, a finite number of meaningless sounds (phonemes) are arranged to make an extensive array of morphemes and words (phonology). Second, morphemes and words are then further organised into myriad compound words, phrases and sentences, which is referred to here as compositional syntax [4,5]. A notable feature of the latter process is that words maintain their identity across compositions, allowing the meaning of the whole to be derived from its parts, and that rules — sometimes referred to as syntactic operations — underpin the association between word composition and information transfer. For example, the word *ship* maintains its basic meaning, and so adds to the meaning of the whole, when preceded by *cargo* or *cruise*, but the constructions lose intended meaning when order is reversed.

Experimental evidence from a handful of social monkey and bird species suggests that the ability to produce compositional sequences is not uniquely human (Figure 1). For example, male Campbell’s monkeys (*Cercopithecus campbelli*) of west Africa use two distinct calls to signal terrestrial versus aerial threats. When the exact threat is ambiguous, however, either alarm can

Figure 1. Disparate taxa show proto compositional syntax.
Playback experiments confirm the essence of compositional syntax is used by primates and unrelated birds in their communication systems: left, Campbell’s monkey (credit Erin Kane); middle, southern pied babbler (credit Dave Humphries); and right, Japanese tit (credit Toshitaka Suzuki).