

partially due to the physical difficulty of gripping and pulling the string through the small hole, and so this question deserves further study.

The results of the new study [6] add to the growing call to 'deconstruct' animal insight into its component parts [11–14]. Rather than simply presenting naïve animals with tricky tasks to see how many can pluck the solution 'out of thin air', researchers have shifted their focus to manipulating an individual's experience and examining how they can generalise from what they have seen or done before to new problems. These studies [10–14] are not about 'insight' as such, but about how animals represent the physical world and the extent to which they can mentally plan or simulate. Differences in these abilities between species may have important consequences for how well they cope when encountering new problems to be solved, for example, when the environment changes [15]. Taylor *et al.* [6] point out that an ability to capitalise on visual feedback concerning the effect of one's actions might be another important ingredient for successful problem-solving. The precise cognitive mechanism by which that is achieved will be an important question for future study; operant conditioning is one possibility, while another is causal learning [16].

So is this, as Taylor *et al.* [6] suggest, an end to insight? Neuroimaging work supports the idea that human insightful problem-solving is a qualitatively distinct (and empirically tractable) mental process, at least in the case of verbal-reasoning problems [17]. When people report having solved problems like puzzle B in Figure 1 through insight rather than through exhaustive search strategies, distinctive patterns of brain activation (for example, in the right anterior superior temporal gyrus) point toward inhibiting the processing of closely-associated but unhelpful information in the left hemisphere, and unconscious activation of distant connections in the right hemisphere, when the solution suddenly 'pops-up' [3].

Perhaps comparative psychologists need to re-visit what a test of 'insight' is trying to capture. In retrospect, the spontaneous solution of the string-pulling problem by naïve birds was always a puzzle: only a minority of human participants solve insight problems as it is, and how many could

solve Maier's two-string task without prior experience with string or heavy objects? An important part of Maier's challenge is to overcome the tendency to view the objects as being fit for a certain purpose. By capitalising on this so-called 'functional fixedness', Maier throws us red-herrings, 'I could stand on the chair', we think, 'or use the spanner to extend my reach'. Only once we have suppressed the obvious uses of the objects do we have a chance of solving the task. Maybe future studies of animal insight could similarly adopt the notion of functional fixedness. If an object is routinely used in one context, will it be harder for animals to use it in a different way to solve a new problem? Fittingly, if one message from the new work is that the current paradigms are better suited to more focussed study of better-defined cognitive abilities (such as the role of visual feedback in problem solving), another is that for the study of insight, comparative researchers are going to need to think outside the box.

References

1. Thorpe, W.H. (1956). *Learning and Instinct in Animals* (London: Methuen & Co).
2. Heinrich, B. (1995). An experimental investigation of insight in common ravens (*Corvus corax*). *Auk*, *112*, 994–1003.
3. Heinrich, B., and Bugnyar, T. (2005). Testing problem solving in ravens: string-pulling to reach food. *Ethology*, *111*, 962–976.
4. Schuck-Paim, C., Borsari, A., and Ottoni, E. (2009). Means to an end: neotropical parrots manage to pull strings to meet their goals. *Anim. Cogn.*, *12*, 287–301.
5. Werdenich, D., and Huber, L. (2006). A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis*. *Anim. Behav.*, *71*, 855–863.
6. Taylor, A.H., Knaebe, B., and Gray, R.D. (2012). An end to insight? New Caledonian crows can spontaneously solve problems without
7. Taylor, A.H., Medina, F.S., Holzhaider, J.C., Hearne, L.J., Hunt, G.R., and Gray, R.D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS ONE*, *5*, e9345.
8. Köhler, W. (1926). *The Mentality of Apes*, 2nd revised Edition (New York: Harcourt, Brace & Company, Inc.).
9. Schiller, P.H. (1952). Innate constituents of complex responses. *Psychol. Rev.*, *59*, 177–191.
10. Völter, C., and Call, J. (2012). Problem solving in great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo abelii*): the effect of visual feedback. *Anim. Cogn.*, *15*, 923–936.
11. Shettleworth, S.J. (2009). Animal cognition: deconstructing avian insight. *Curr. Biol.*, *19*, R1039–R1040.
12. von Bayern, A.M.P., Heathcote, R.J.P., Rutz, C., and Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Curr. Biol.*, *19*, 1965–1968.
13. Seed, A.M., and Byrne, R.W. (2010). Animal tool-use. *Curr. Biol.*, *20*, R1032–R1039.
14. Cheke, L., Bird, C., and Clayton, N. (2011). Tool-use and instrumental learning in the Eurasian jay (*Garrulus glandarius*). *Anim. Cogn.*, *14*, 441–455.
15. Seed, A.M., and Call, J. (2010). Physical problem solving in tool-using and non-tool-using animals. In *Encyclopedia of Animal Behaviour*, Volume 2, M. Breed and J. Moore, eds. (Oxford: Academic Press), pp. 778–785.
16. Blaisdell, A.P., Sawa, K., Leising, K.J., and Waldmann, M.R. (2006). Causal reasoning in rats. *Science*, *311*, 1020–1022.
17. Bowden, E.M., Jung-Beeman, M., Fleck, J., and Kounios, J. (2005). New approaches to demystifying insight. *Trends Cogn. Sci.*, *9*, 322–328.
18. Maier, N.R.F. (1931). Reasoning and learning. *Psychol. Rev.*, *38*, 332–346.
19. Jung-Beeman, M., Bowden, E.M., Haberman, J., Frymiare, J.L., Arambel-Liu, S., Greenblatt, R., Reber, P.J., and Kounios, J. (2004). Neural activity when people solve verbal problems with insight. *PLoS Biol.*, *2*, e97.

¹School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, St Andrews, KY16 9JP, UK.
E-mail: ams18@st-andrews.ac.uk

<http://dx.doi.org/10.1016/j.cub.2012.11.043>

Visual Attention: Bringing the Unseen Past into View

Attention facilitates perception and can bring stimuli too faint to see into consciousness. A new study shows that attention can reach into the past, acting on the memory trace of a stimulus that has disappeared before being attended.

Robert W. Kentridge

Attention acts by facilitating the processing of selected parts of the world. Visually we might attend only to stimuli that are on the left side of space.

In experimental studies of attention, a cue is typically used to tell observers where to attend, such as a flashing spot on one side of a display [1]. The effects of attention vary with the delay between presentation of the cue and of

the target stimuli that attention acts on. Attention takes time to act and so the cue must typically be presented before the targets to facilitate perception of the target. For some types of cue, attention acts for a limited duration and its effects disappear, even reversing into an impairment of perception, if the delay between presentations of the cue and targets is long. Our current understanding is that attention must be brought into action in advance of the stimuli it is going to act on. Indeed, when there is a question of whether cues in a task are producing an effect simply by virtue of their own sensory properties rather than by directing attention, a standard control involves presenting the cues *after* the target in order to measure their effects independent of attention [2]. The study reported in this issue of *Current Biology* by Sergent *et al.* [3] is the first to show that a cue presented after a target can produce a selective attentional effect on the memory trace of the target. This finding not only suggests that our understanding of attention needs to be revised, but also has implications for theories about visual consciousness.

Sergent *et al.* [3] used a simple design where attention was directed to one of two spatial locations indicated by circles on a computer display. One of the circles briefly dimmed slightly, indicating the attended location. The target was a briefly presented, low-contrast Gabor patch (essentially a patch of fuzzy straight lines) at one of the locations. The observer's task was to report the orientation of the Gabor patch, choosing between one of two alternatives presented at the end of each trial. The location at which the target had actually been presented was indicated at the end of the trial so, at the time the observer made their judgement, there was no uncertainty over the target location. That judgment could, however, be influenced by the effect of attention on processing visual signals elicited at the time the target was presented. The effect of cueing was assessed by comparing the accuracy of judgments between trials where the target appeared at the cued location with trials where it appeared at the other location. This difference was measured over a range of delays between presentations of cues and targets.

The results showed the cueing effect increasing as the interval between cue and target presentation decreased

from 400 ms to 100 ms (typical for 'exogenously' cued spatial attention). Sergent *et al.* [3] also tested delays where the cue *followed* the target; they continued to find cueing effects when the cue appeared up to 400 ms *after* the target had disappeared from the display. This extraordinary finding may have been made possible by the type of cues used. Typically, a highly salient cue would be used to maximise the capture of attention. Such salient cues presented soon after a faint target would, in addition to any attentional effect, act as an effective mask, interfering with perception of the target. In Sergent *et al.*'s [3] task, the cue was a weak dimming of the circle at the cued-location which would only produce minimal masking.

Attending to a stimulus can increase its salience. Attended stimuli appear to have a higher contrast than physically identical unattended stimuli. When the contrast of a stimulus is just below the threshold of visibility this increase in salience can allow an observer to see a stimulus that would otherwise be invisible [4]. Sergent *et al.*'s [3] second experiment examined the effect of attention on the visibility of targets at threshold. In addition to the objective target orientation judgement, observers also provided a subjective rating of the target's visibility. Signal detection analyses show that attention increased sensitivity to targets both when cues preceded and followed the targets. Estimates of the proportion of consciously visible targets were larger for attended than unattended targets — retrospectively acting cues appear to bring targets that would have been unseen into consciousness. These increases in subjective visibility were accompanied by better performance in the objective orientation discrimination task.

Although the new study does not directly address underlying mechanisms, the effect must depend on attention acting on some neural trace that persists after the offset of the target. We know that attention modifies the neural response elicited by targets [5] so it is, perhaps, unsurprising that attention can affect neural responses that continue after target offset. Neural activity elicited by transient visual stimuli persists for long periods [6]. What is surprising is that retro-active attention brings otherwise unseen stimulus into consciousness.

Attention plays a role in many theories of consciousness. Both Lamme [7] and Dehaene *et al.* [8] propose that attention can amplify the neural trace of a stimulus so that it has long-lasting effects spreading from sensory areas of cortex to frontal regions. They accommodate findings that attention can act on stimuli that do not elicit consciousness [9] by suggesting that attention only promotes stimuli to conscious report whose sensory neuronal representation persists through feedback of signals between areas. When attention produces a behavioural effect in the absence of consciousness the strength of neural response is enhanced but no recurrent feedback takes place. They differ in their views on unattended stimuli that elicit recurrent processing restricted to sensory areas: Lamme [7] leaves open the possibility that these too might produce conscious experience, whereas Dehaene *et al.* [8] refer to them as 'preconscious'. The neural traces that attention acts on in Sergent *et al.*'s [3] experiments persist for so long that they are likely to depend on feedback of neural signals, so it appears that without attention these recurrent signals do not elicit consciousness, as Dehaene *et al.* suggest.

The philosopher Ned Block [10], however, distinguishes between two forms of consciousness: *phenomenal consciousness*, which corresponds to the experience elicited by a stimulus, and *access consciousness*, in which the properties of the stimulus become available to cognitive processes. Block suggests that recurrent signalling that remains restricted to posterior areas generates phenomenal consciousness, with access consciousness only conferred on the posterior signal that wins the competition to spread forward frontally. He explains that "the strong but still losing coalitions in the back of the head are the neural basis of phenomenal states (so long as they involve recurrent activity)" ([10] p. 499).

Block's [10] position originates from consideration of a 1960 study (reminiscent of that of Sergent *et al.* [3]) by George Sperling [11]. In the 'partial report' experiment observers are presented with a rectangular grid of a dozen letters, arranged in three rows of four, that is displayed for only 50 ms. They must identify as many of the letters as possible. The task is hard and most observers only manage to report

about four letters. If, however, they are instructed to report as many letters as possible from one particular row then, even if the instruction is given just *after* the letters were presented, observers usually manage to report the complete row of four letters. It seems that all of the letters are potentially reportable, but only four can actually be reported. The cue instructs the observer which four to select.

Block [10] emphasises that observers have the impression they see all of the letters even though they cannot report all their identities. He claims that the experience of the unreported items is complete — it is not a matter of seeing ‘blurs’ or generic impressions of letters, but rather seeing all of the letters in the array with equal levels of phenomenal detail despite only able to access the identity of the reported subset. Items can exist that are seen phenomenally but whose identity cannot be reported because the capacities of phenomenal and access consciousness differ.

The contrary position, for example [12], is that experience of the unreported items is incomplete and so there is no dissociation between experience and cognitive access.

For this to occur we need to have, in Block’s own words ([13] p. 573), “unconscious representations that are specific enough to do the task with the observed accuracy... the cue is supposed to promote attentional amplification of the cued unconscious specific representation, which, when combined with the conscious generic representation, results in a conscious specific representation of the cued item.” That is, of course, exactly what Sergent *et al.* [3] have found (except that their subjects do not even appear to report a generic representation of the unseen stimulus).

Sergent *et al.*’s [3] result does not necessarily invalidate the distinction between access and phenomenal consciousness, but it does lend weight to the alternative, and perhaps simpler, position that consciousness is just consciousness.

References

1. Posner, M.I. (1980). Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25.
2. Carrasco, M. (2011). Visual attention: the past 25 years. *Vision Res.* 51, 1484–1525.
3. Sergent, C., Wyart, V., Babo-Rebello, M., Cohen, L., Naccache, L., and Tallon-Baudry, C. (2012). Cueing attention after the stimulus is gone can retrospectively trigger conscious perception. *Curr. Biol.* 23, 150–155.

4. Carrasco, M., Ling, S., and Read, S. (2004). Attention alters appearance. *Nat. Neurosci.* 7, 308–313.
5. Motter, B.C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* 70, 909–919.
6. Offen, S., Schluppeck, D., and Heeger, D.J. (2009). The role of early visual cortex in visual short-term memory and visual attention. *Vision Res.* 49, 1352–1362.
7. Lamme, V.A.F. (2006). Towards a true neural stance on consciousness. *Trends Cogn. Sci.* 10, 494–501.
8. Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., and Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10, 204–211.
9. Kentridge, R.W., Nijboer, T.C.W., and Heywood, C.A. (2008). Attended but unseen: Visual attention is not sufficient for visual awareness. *Neuropsychologia* 46, 864–869.
10. Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behav. Brain Sci.* 30, 481–548.
11. Sperling, G. (1960). The information available in brief visual presentation. *Psychol. Monogr. Gen. Appl.* 74, 1–29.
12. Cohen, M.A., and Dennett, D. (2011). Consciousness cannot be separated from function. *Trends Cogn. Sci.* 15, 358–364.
13. Block, N. (2011). Perceptual consciousness overflows cognitive access. *Trends Cogn. Sci.* 15, 567–575.

Department of Psychology, Durham University, Durham DH1 3LE, UK.
E-mail: robert.kentridge@durham.ac.uk

<http://dx.doi.org/10.1016/j.cub.2012.11.056>

Adaptive Radiation: Convergence and Non-equilibrium

The spectacular adaptive radiation of cichlid fish in Lake Tanganyika encompasses extensive morphological convergence and co-occurrence of ecologically similar species, forcing a reevaluation of non-equilibrium dynamics in community assembly.

Rosemary G. Gillespie

The diversity of life is bewildering, but two age-old questions remain: first, is species origination dictated by chance evolutionary events or constrained to follow fairly predictable trajectories? Second, does the observed diversity and composition of species reflect an equilibrium, and if so, over what time period? In terms of species origin, one argument is that evolutionary outcomes are shaped by the whims of immediate events: “The divine tape player holds a million scenarios ... [and] the end results are so different” [1]. The alternative is that outcomes are

constrained such that the appearance of certain forms at a given time and place becomes “very probable, if not inevitable” [2]. With regards to patterns of species composition, the debate concerns the ‘balance of nature’ — the idea that the overall diversity at a site tends toward a relatively steady state. This supposition was questioned with the recognition of the importance of the dynamic nature of biodiversity, and that patterns may be governed more commonly by non-equilibrium processes in which species diversity is inherently unstable and changing over time.

Insights into these long-standing questions, as often in evolutionary biology, have come from insular systems, habitats isolated by surroundings that are inhospitable to the respective organisms, as these provide discrete settings, often replicated over space and time. Moreover, with the advent of sophisticated genomic, isotopic, and visualization tools, it has become possible to understand the detailed history of lineages, and the extent to which patterns of differentiation are linked to shifts in ecology and associated morphology. In a recent issue of *Current Biology*, Muschick *et al.* [3] summarize the results of an extraordinarily comprehensive study of the adaptive radiation of cichlid fish in the African Great Lakes, in which the ecological identity of species, and their occurrence within a given community, is frequently predictable. The study represents the most extensive quantitative analysis to date