

therefore emerges whereby one of the key functions of the intact basal ganglia is to link positive outcomes to subsequent behaviour, whether predominantly cognitive or motor in its demands, and to modify this relationship according to motivational state.

Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/15/R648/DC1>

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References

- Niv, Y. (2007). Cost, benefit, tonic, phasic: what do response rates tell us about dopamine and motivation? *Ann. NY Acad. Sci.* 1104, 357–376.
- Satoh, T., Nakai, S., Sato, T., and Kimura, M. (2003). Correlated coding of motivation and outcome of decision by dopamine neurons. *J. Neurosci.* 23, 9913–9923.
- Brown, P., Chen, C.C., Wang, S., Kühn, A.A., Doyle, L., Yarrow, K., Nuttin, B., Stein, J., and Aziz, T. (2006). Involvement of human basal ganglia in off-line feed-back control of voluntary movement. *Curr. Biol.* 16, 2129–2134.
- Hamani, C., Saint-Cyr, J.A., Fraser, J., Kaplitt, M., and Lozano, A.M. (2004). The subthalamic nucleus in the context of movement disorders. *Brain* 127, 4–20.
- Frank, M.J., Seeberger, L., and O'Reilly, R.C. (2004). By carrot or by stick: Cognitive reinforcement learning in Parkinsonism. *Science* 306, 1940–1943.
- Shohamy, D., Myers, C.E., Onlaor, S., Grossman, S., Sage, J., Gluck, M.A., and Poldrack, R.A. (2004). Cortico-striatal contributions to feedback-based learning: Converging data from neuroimaging and neuropsychology. *Brain* 127, 851–859.
- Kempf, F., Brücke, C., Kühn, A.A., Schneider, G.H., Kupsch, A., Chen, C.C., Androulidakis, A.G., Wang, S., Vandenbergh, W., Nuttin, B., et al. (2007). Modulation by dopamine of human basal ganglia involvement in feedback control of movement. *Curr. Biol.* 17, R587–R589.
- O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., and Dolan, R.J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science* 304, 452–454.
- Wrase, J., Kahnt, T., Schlagenhauf, F., Beck, A., Cohen, M.X., Knutson, B., and Heinz, A. (2007). Different neural systems adjust motor behavior in response to reward and punishment. *Neuroimage* 36, 1253–1262.
- Tricomi, E.M., Delgado, M.R., and Fiez, J.A. (2004). Modulation of caudate activity by action contingency. *Neuron* 41, 281–292.

¹Department of Neurology and ²Department of Neurosurgery, Charité-University Medicine Berlin, CVK, Berlin, Germany. ³Sobell Department of Motor Neuroscience and Movement Disorders, Institute of Neurology, London, UK. ⁴Department of Neurosurgery, Kings College Hospital, Denmark Hill, London, UK. ⁵Department of Physiology, Anatomy and Genetics and ⁶Department of Neurological Surgery, Radcliffe Infirmary, Oxford, UK. ⁷Department of Neurology and ⁸Neurosurgery, Katholieke Universiteit Leuven, Belgium. E-mail: p.brown@ion.ucl.ac.uk

The sound of change: visually-induced auditory synesthesia

Melissa Saenz and Christof Koch

Synesthesia is a benign neurological condition in humans characterized by involuntary cross-activation of the senses, and estimated to affect at least 1% of the population [1]. Multiple forms of synesthesia exist, including distinct visual, tactile or gustatory perceptions which are automatically triggered by a stimulus with different sensory properties [1–6], such as seeing colors when hearing music. Surprisingly, there has been no previous report of synesthetic sound perception. Here we report that auditory synesthesia does indeed exist with evidence from four healthy adults for whom seeing visual flashes or visual motion automatically causes the perception of sound. As an objective test, we show that ‘hearing-motion synesthetes’ outperformed normal control subjects on an otherwise difficult visual task involving rhythmic temporal patterns similar to Morse code. Synesthetes had an advantage because they not only see, but also hear the rhythmic visual patterns. Hearing-motion synesthesia could be a useful tool for studying how the auditory and visual processing systems interact in the brain.

All four of the synesthete subjects (S1–S4, ages 23–33, 1 woman) had normal visual acuity and no known hearing or neurological deficits. Their visually-induced sound perceptions occur automatically, cannot be turned off, and have been experienced for as long as they can remember going back into childhood. The percepts are typically simple, non-linguistic sounds (such as beeping, tapping or whirring) that are temporally associated with visual flashes or continuous visual motion. Eye movements over a stationary scene (retinal motion) do not typically evoke sound. In daily experience, all four subjects are generally able to distinguish their synesthetic sound percepts from percepts induced by real auditory stimuli, but occasional confusion exists. We refer to this phenomenon as ‘hearing-motion’ synesthesia, even though non-moving visual flashes also trigger sound perception as demonstrated next.

Our goal was to devise a task for which hearing-motion synesthesia would confer a performance *advantage*, as this would be strong objective evidence for the perceptual experience [4]. Typically (in non-synesthetes), people have an advantage in judging rhythmic patterns of sound compared to equivalent visual rhythmic patterns [7,8]. We thus predicted that synesthetes would perform *better* than controls in a task involving visual rhythmic sequences because synesthetes would not only see, but also hear the patterns.

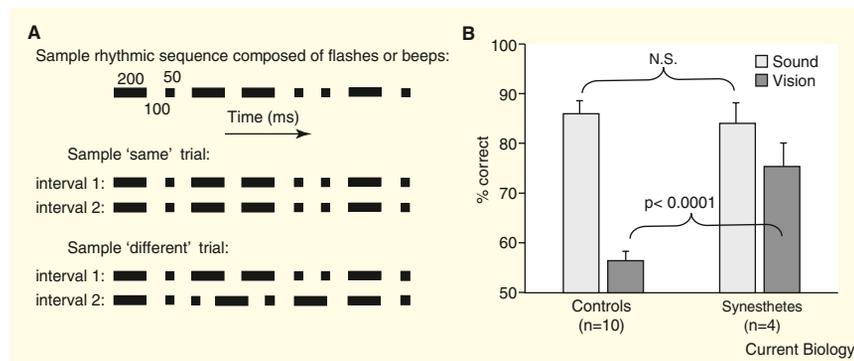


Figure 1. Visually-induced auditory synesthesia.

(A) Sequences were composed of intermixed long (200 ms) and short (50 ms) duration stimuli separated by blank intervals (100 ms) similar to Morse code (bars depict stimulus on-times). The stimuli were either tonal beeps (360 Hz) on sound trials or centrally flashed discs (1.5 deg radius) on visual trials. On each trial, subjects judged whether two successive sequences (either both sound or both visual) were the ‘same’ or ‘different’. (B) Mean performance (% correct trials) for control and synesthete subjects (+/– SEM). All subjects had good accuracy on sound trials, but synesthetes dramatically outperformed controls on the otherwise difficult visual trials. Movies of sample trials located online at <http://www.klab.caltech.edu/~saenz/hearing-motion.html>.

Four synesthetes and ten age-matched control subjects were presented with rhythmic temporal sequences composed of either auditory beeps or of visual flashes (Figure 1). On each trial, subjects judged whether two successive sequences (either both auditory or both visual) were the 'same' or 'different' sequences. Sound and visual trials (100 trials per subject) were randomly interleaved. On sound trials, both groups performed equally well (controls: 85.8% correct; synesthetes: 83.9%, no statistical difference between groups, $p = 0.7$). However, on visual trials control performance fell to near 50% chance level, while synesthetes maintained accurate performance (controls 56.3%; synesthetes 75.2%, highly significant difference between groups $p < 0.0001$). Synesthetic sounds were not as effective as the actual beeps on sound trials in facilitating task performance, consistent with the synesthetes' subjective report (difference between sound and visual scores, controls: $p < 0.0001$; synesthetes: $p = 0.01$). Results were highly consistent at the individual subject level — each control subject performed significantly worse on visual compared to sound trials (range of p -values: $p = 0.02$ to $p < 0.0001$), but individual synesthetes did not (S1 $p = 0.1$, S2 $p = 0.1$, S3 $p = 0.2$, S4 $p = 0.3$; see Supplemental Figure S1 in the Supplemental data available on-line with this issue). A binomial test was used for all statistical comparisons.

Indeed, all synesthetes reported distinct sound perceptions (beeps or taps) associated with each flash on visual trials and using that sound to perform the task. Three out of the four synesthetes reported a change in the tonal quality (but not the strength or consistency) of the associated sound over the brief time course of the experiment. Their synesthetic sounds become more similar to the actual beep given on sound trials as they came to associate that sound with the experiment. Thus, the exact audio-visual association may be alterable, in contrast to other synesthetic associations that are reportedly stable over time ([1,6]; but see [9]).

Hearing-motion synesthesia could be useful for studying how the auditory and visual systems interact in the brain [7,10]. This synesthesia combines perceptions that are temporally linked in normal

experience — objects that move or appear suddenly, such as a bee buzzing or a car whizzing past, often do make a sound. Indeed, our results suggest a strong audiovisual temporal correspondence. Furthermore, previous work suggests that the brain may normally translate the temporal structure of visual information into an auditory representation in order to improve temporal judgments of visual input [7]. Further study could reveal whether hearing-motion synesthesia represents an exaggerated form of normal interactions between auditory and visual systems and whether synesthetic sound perception is associated with activation of the auditory cortex.

Supplemental data

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References

1. Simner, J., Mulvenna, C., Sagiv, N., Tsakanikos, E., Witherby, S.A., Fraser, C., Scott, K., and Ward, J. (2006). Synaesthesia: the prevalence of atypical cross-modal experiences. *Perception* 35, 1024–1033.
2. Banissy, M.J., and Ward, J. (2007). Mirror-touch synesthesia is linked with empathy. *Nat. Neurosci.* 10, 815–816.
3. Beeli, G., Esslen, M., and Jancke, L. (2005). Synaesthesia: when coloured sounds taste sweet. *Nature* 434, 38.
4. Ramachandran, V.S., and Hubbard, E.M. (2001). Psychophysical investigations into the neural basis of synaesthesia. *Proc. Biol. Sci.* 268, 979–983.
5. Rich, A.N., and Mattingley, J.B. (2002). Anomalous perception in synaesthesia: a cognitive neuroscience perspective. *Nat. Rev. Neurosci.* 3, 43–52.
6. Baron-Cohen, S., Wyke, M.A., and Binnie, C. (1987). Hearing words and seeing colours: an experimental investigation of a case of synaesthesia. *Perception* 16, 761–767.
7. Guttman, S.E., Gilroy, L.A., and Blake, R. (2005). Hearing what the eyes see: auditory encoding of visual temporal sequences. *Psychol. Sci.* 16, 228–235.
8. Glenberg, A.M., Mann, S., Altman, L., Forman, T., and Prociase, S. (1989). Modality effects in the coding and reproduction of rhythms. *Mem. Cognit.* 17, 373–383.
9. Ward, J., and Mattingley, J.B. (2006). Synaesthesia: an overview of contemporary findings and controversies. *Cortex* 42, 129–136.
10. Saenz, M., Lewis, L.B., Huth, A.G., Fine, I., and Koch, C. (2008). Visual motion area MT+/V5 responds to auditory motion in human sight-recovery subjects. *J. Neurosci.* 28, 5141–5148.

Division of Biology, Caltech, Pasadena, California 91125, USA.
E-mail: saenz@caltech.edu

Near-future levels of ocean acidification reduce fertilization success in a sea urchin

Jon N. Havenhand¹, Fenina-Raphaella Buttler², Michael C. Thorndyke³ and Jane E. Williamson²

Although it is widely believed that seawater is chemically well-buffered, CO₂-induced acidification of the world's oceans threatens the viability of many species [1–3]. Research to date has focused on the responses of adult stages of calcifying taxa to gross pH changes relevant for the years 2200–2400 [3,4]. We investigated the consequences of exposure of gametes and larvae of the sea urchin *Helicodaris erythrogramma* to CO₂-induced acidification by –0.4 pH units (the upper limit of predictions for the year 2100 [5]), and found statistically significant reductions in sperm swimming speed and percent sperm motility. We predicted the effects of these changes using an established model [6], and tested fertilization success experimentally in assays using the same gametes and pH treatments. Observed reductions in fertilization success corresponded closely to model predictions (24% reduction). If general, these findings have important implications for the reproductive and population viability of broadcast spawning marine species in the future acidified ocean.

During the 20th century, rising atmospheric CO₂ has reduced surface ocean pH by 0.1 units and carbonate concentrations by 30 $\mu\text{mol kg}^{-1}$ [7]. Modelling shows that these changes will accelerate in the coming century [5], increasing the solubility of biogenic calcareous structures and threatening the survival of keystone calcifying species [2,4,8]. The broader physiological and ecosystem-level consequences of these changes are of acute concern [8,9], but there are few relevant data available and the likely repercussions are almost wholly unknown [1]. Critically, there are no published data on the likely effects of increased CO₂ on fertilization and