

facial expressions, whenever amygdala activation has been demonstrated in the absence of conditioned fear, subjects have not been required to make a forced-choice response about the nature of the unseen expression. That is, they were not engaged in the sort of guesswork undertaken by blindsight patients. It is plausible that GY, a much-practised observer, is able to monitor his autonomic responses and use them to mediate above-chance performance in the discrimination of facial expression. However, the differential responses of the amygdala to different facial expressions² is consistent with its role in the processing of at least some facial expressions. The rapidity with which the responses to unmasked fear-conditioned stimuli desensitize¹² leaves open the possibility that repeated presentation could mitigate against GY's performance. Moreover, it remains an interesting possibility that an improvement in performance might have been obtained had GY been asked to make a reflexive response, such

as a key press, which is less likely than verbalization to invoke reflective conscious processes. The genuine guesses of an uninformed conscious system might potentially interfere with the stimulus-driven responses of the putative collicular circuit. We will have to wait for further experiments to answer this question.

References

- 1 Whalen, P.J. et al. (1998) Masked presentation of emotional facial expressions modulate amygdala activity without explicit knowledge. *J. Neurosci.* 18, 411–418
- 2 Blair, R.J.R. et al. (1999) Dissociable neural responses to facial expressions of sadness and anger. *Brain* 122, 883–893
- 3 de Gelder, B. et al. (1999) Non conscious recognition of affect in the absence of striate cortex. *NeuroReport* 10, 3759–3763
- 4 Morris, J.S. et al. (1999) A subcortical pathway to the right amygdala mediating 'unseen' fear. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1680–1685

- 5 Weiskrantz, L. (1997) *Consciousness Lost and Found*, Oxford University Press
- 6 Dehaene, S. et al. (1998) Imaging unconscious semantic priming. *Nature* 395, 597–600
- 7 Marcel, A.J. (1998) Blindsight and shape perception: deficit of visual consciousness or of visual function? *Brain* 121, 1565–1588
- 8 Bassili, J.N. (1979) Emotion recognition: the role of facial movement and the relative importance of upper and lower areas of the face. *J. Pers. Soc. Psychol.* 37, 2049–2058
- 9 Soken, N.H. and Pick, A.D. (1992) Intermodal perception of happy and angry expressive behaviors by 7-month-old infants. *Child Dev.* 63, 787–795
- 10 Adolphs, R. et al. (1994) Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature* 372, 669–672
- 11 Calder, A.J. et al. (1996) Facial emotion recognition after bilateral amygdala damage. *Cognit. Neuropsychol.* 13, 699–745
- 12 Büchel, C. et al. (1998) Brain systems mediating aversive conditioning: an event-related fMRI study. *Neuron* 20, 947–957

Affective blindsight: are we blindly led by emotions?

Response to Heywood and Kentridge (2000)

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The recent findings that facial expression can be recognized in the absence of awareness by blindsight patients suggests that, as the saying goes, we might indeed be blindly led by emotions. Although we are entirely in agreement with the comments made by Heywood and Kentridge [Heywood, C.A. and Kentridge, R.W. (2000) Affective blindsight? *Trends Cognit. Sci.* 4, 125–126]¹ we would like to take this opportunity to discuss some of the questions that they raised and to describe our most recent data that may clarify some of the important issues.

As Heywood and Kentridge remark, the finding of covert discrimination by a blindsight subject of facial expressions presented to his blind field ('affective blindsight') raises the question of how this performance is achieved. An fMRI approach should provide new evidence with regard to the actual pathways sustaining affective blindsight, but it is worth noting that behavioral experiments can also help to clarify the neural basis of this phenomenon; for example, by determining which stimulus categories and attributes can be processed in the absence of striate cortex. Indeed, our most recent results indicate that blindsight is found only for facial expression and that covert discrimination of other facial attributes

such as personal identity, gender and facial speech are not observed².

This pattern is consistent with the explanation suggested by Heywood and Kentridge that the biological or ecological salience of a stimulus is more important than the degree of visual complexity *per se* when deciding whether a given stimulus will support blindsight. However, if this were the only critical factor one might expect facial speech to support blindsight. Indeed, natural language, certainly when taken at the level of basic phoneme and syllable discrimination, is an integral part of our basic biological make-up. So it was something of a surprise that we were unable to find any indication of a capacity for discriminating or identifying facial speech in blindsight patients. One possible explanation rests upon the size of the stimuli used. There is evidence that spatial resolution is poor in blindsight, and so stimulus size is likely to be crucial. Perhaps discrimination of facial speech was not found because the lower part of the face contains relatively small stimulus features. It remains to be seen whether a very large lip-reading stimulus would support blindsight.

More importantly though, this negative result does seem to pose problems for Heywood and Kentridge's suggestion that movement might be one of the criti-

cal factors in explaining the findings. This suggestion was based upon our earlier finding that, although moving images supported affective blindsight, stationary images did not. This is consistent with findings that demonstrate that discriminating between two patterns of biological movement can be done on the basis of very limited or very impoverished input. But if movement is important, why does facial speech not support blindsight? In facial speech, one has a stimulus that is socially and biologically significant and for which discrimination can be done on the basis of the same kind of impoverished information consisting of a small number of moving dots³.

Whatever the outcome of that particular debate we do now have some preliminary evidence suggesting that stationary images of facial expressions can support affective blindsight (de Gelder et al., unpublished data). In our experiment, we measured the impact of a face presented to the blind field on the response to a facial stimulus presented to the intact, seeing field. The results showed that incongruity between the expressions presented to the two hemifields significantly delayed judgement of the facial expression in the seeing field.

This is an illustrative example that covert processing can often only be found with an indirect rather than a direct method, in which subjects are required to 'guess' the identity of stimuli they patently deny seeing. As Heywood and Kentridge suggest – in line with some recent findings about qualitative differences between overt and covert processes – the superior sensitivity of indirect methods for uncovering covert processing or residual processing abilities might be due to an absence of conflict between overt, reflexive answering and covert responding. We addressed

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just this issue by using false response labels in one of our experiments (Experiment 4). The results came as a bit of a surprise. One of us stubbornly reasoned that as a test for implicit learning of discriminative cues we should ask GY to respond using false response labels – that is, emotional labels that do not correspond to the emotions expressed in the stimuli. This might yield results showing that affective stimuli were labelled systematically and, thus, that associative learning had occurred. This was not found. Instead, when instructed with non-veridical alternatives, GY's performance was completely un-systematic and at chance level. Affective blindsight therefore does not appear to be explained by implicit learning. After all, it is unlikely that through untutored, unsupervised implicit learning GY would hit upon the correct solution – a solution that reflects a three-way equation between the stimulus, its conscious meaning and its non-conscious meaning.

The above considerations suggest that the issue of the relative sensitivity of various testing methods is more than a quantitative matter, and in fact involves a qualitative capacity for stimulus

identification. Heywood and Kentridge raise a very interesting issue when asking whether key-press responses could have strengthened the data further (in fact, that is what we did use). They speculate that with reflexive verbal responses, the response generated in the blind field via dedicated routes could be inhibited by mechanisms of awareness. The finding that non-veridical response alternatives have a negative effect on the results of guessing suggests, paradoxically, that awareness plays a role in covert recognition. For example, the underlying mechanism might be one of conscious processes monitoring autonomous reactions, as indeed Heywood and Kentridge suggest.

But there might be other reasons why indirect paradigms are more sensitive than direct paradigms and why different response modalities yield different results. Neuropsychological subjects are, by definition, unaware of the capacities that can be revealed by experiments on their implicit processes. 'Direct' methods require them to engage in discriminations that they do not believe they can make. In such a counterintuitive situation, subjects (and some experimenters!) might be less than willing to

accept that there is any point in continued vigilance with forced-choice guessing. Indirect methods completely remove this counterintuitive element.

Further research is needed to discover whether affective blindsight is restricted to emotions for which the amygdala is at present known to play a special role. But even if the amygdala's role is specific only to particular emotional stimuli or states, and other emotional states depend critically on other targets, our results suggest that these too can be assumed to be well-provided for in terms of visual projections via the sub-cortical collicular–pulvinar route (among others) that bypass the primary visual cortex.

References

- 1 Heywood, C.A. and Kentridge, R.W. (2000) Affective blindsight? *Trends Cognit. Sci.* 4, 125–126
- 2 Rossion, B. et al. Early extrastriate activity without primary visual cortex. *Neurosci. Lett.* (in press)
- 3 Rosenblum, L.D. et al. (1996) Point-light facial displays enhance comprehension of speech in noise. *J. Speech Hear. Res.* 39, 1159–1170

Homologies for numerical memory span?

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For some, the case of Clever Hans represents the kind of trap that animal researchers often fall into when searching for human capacities in other creatures. Hans was certainly clever with respect to picking up on human cues, but was unquestionably clueless when it came to solving mathematical problems. Ever since the debunking of Clever Hans, however, an extraordinary amount of evidence has accumulated^{1,2}, showing beyond a shadow of doubt, that we share many of the core building blocks of our number capacity with other animals. We know, for example, that several avian (pigeon, African gray parrot) and mammalian (rat, rhesus monkey, chimpanzee) species can be trained to classify sets of objects with respect to their ordinal relationships, appreciate that number is property indifferent (i.e. as long as the object or event is an entity that can be counted or individuated, its properties are irrelevant), and that there is a one-to-one correspondence between the numerical tag and the object counted. There is also evidence that monkeys show a certain level of numerical sophistication in the absence of training. Specifically, using techniques that are analogous to those used with

human infants, cotton-top tamarins and rhesus monkeys have been shown to compute simple arithmetical operations such as additions and subtractions. Now, in an exciting new report in *Nature*³, Kawai and Matsuzawa add to our growing understanding of the evolutionary origins of the human capacity for number by showing that a chimpanzee has a numerical memory span that falls well within the range of the 'magic number 7', at least on some accounts⁴.

Kawai and Matsuzawa worked with their star chimpanzee, a female by the name of 'Ai' with over 20 years of experimental experience. Prior to conducting the current study, Matsuzawa had shown that Ai could learn the Arabic numerals from 0 to 9. Specifically, based on extensive training, Ai had learned to respond on a touch-sensitive monitor to the ordinal relationships between numbers. Thus, when shown a sequence of four numbers, with inter-integer differences of either one or more, she would touch each number from lowest to highest, and with remarkable speed and accuracy. Taking advantage of this ability, Kawai and Matsuzawa set up a memory span task. A set of numbers was displayed on a monitor, such as 1,3,4,6,9.

As soon as Ai pressed the first number in the sequence (i.e. 1), all of the remaining numbers were masked by a white square. Ai's task was to press the remaining numbers (now masked) in order. For set sizes of two to four numbers, her performance was above 90% correct. Although her performance dropped to 65% for set sizes of five, this was nonetheless significantly above chance (i.e. 4%; note that in the original manuscript this was incorrectly calculated as 6%). Of considerable interest was her reaction time to respond. Independent of set size, Ai was slowest on the first press, with reaction time remaining relatively constant for all subsequent responses. Thus, for example, mean reaction time for the first response to a set size of four was 717 ms, and then 390, 432, and 437 respectively for the last three, masked, responses. This strongly suggests that Ai first explored the number space, calculating the ordinal relationships and spatial locations of each number, and then used this stored information to guide her subsequent responses.

As in all well-designed research with interesting results, many questions remain. To understand better whether Ai's capacity for calculating ordinal

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