

Preserved complex emotion-based learning in amnesia

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Abstract

An important role for emotion in decision-making has recently been highlighted by disruptions in problem solving abilities after lesion to the frontal lobes. Such complex decision-making skills appear to be based on a class of memory ability (emotion-based learning) that may be anatomically independent of hippocampally mediated episodic memory systems. There have long been reports of intact emotion-based learning in amnesia, arguably dating back to the classic report of Claparede. However, all such accounts relate to relatively *simple* patterns of emotional valence learning, rather than the more complex contingency patterns of emotional experience, which characterise everyday life. A patient, SL, who had a profound anterograde amnesia following posterior cerebral artery infarction, performed a measure of complex emotion-based learning (the Iowa Gambling Task) on three separate occasions. Despite his severe episodic memory impairment, he showed normal levels of performance on the Gambling Task, at levels comparable or better than controls—including learning that persisted across substantial periods of time (weeks). Thus, emotion-based learning systems appear able to encode, and sustain, more sophisticated patterns of valence learning than have previously been reported.

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Patients with substantial lesions to the frontal lobes often show relatively normal intelligence, and near-normal performance on a range of traditional executive measures, such as the Wisconsin Card Sorting Task and Tower of Hanoi/London (Bechara, Damasio, Damasio, & Anderson, 1994; Damasio, 1996). However, in spite of normal performance on 'executive' tasks, such patients often choose unsuitable friends, enter inadvisable relationships and engage in ill-advised activities (Bechara et al., 1994; Damasio, 1996; Manes et al., 2002; Rogers et al., 1999; Rolls, Hornack, Wade, & McGrath, 1994). It has been proposed that these poor judgement and decision-making abilities in social cognition follow from an inability to use emotion-based knowledge about the possible outcome of decisions (Bechara, Damasio, & Damasio, 2000; Damasio, 1994, 1996; LeDoux, 2000; Rolls et al., 1994; Turnbull, Berry, & Bowman, 2003, though see Tomb, Hauser, Deldin, & Caramazza, 2002 for a dissenting voice).

A number of different measures have been designed to assess emotion-based learning, for example the Cambridge Gambling Task (Rogers et al., 1999) and tasks of delayed discounting (Bickel, Degrandpre, & Higgins, 1995; Bowman & Turnbull, 2004). However, much of the research has focused on one measure, the Iowa Gambling Task (Bechara et al., 1994; Bechara, Tranel, Damasio, & Damasio, 1996; Bechara, Damasio, Tranel, & Damasio, 1997; Bechara et al., 2000). Here, the participant is faced with four decks of cards, and asked to choose any deck, in any sequence. They win or lose money with each card turn. Some decks have high gains, but also substantial losses, such that sustained playing leads to overall financial loss. Other decks have more modest payouts, but produce smaller losses, so that sustained playing leads to small but consistent gains. The claim that learning on such measures is somehow related to *emotion* systems (rather than other classes of non-declarative memory) is based on a range of factors: notably that such tasks involve an explicit regime of reward and punishment (Bechara et al., 2000) produce modifications in skin-conductance findings while the task is being played (e.g., Bechara, Damasio, Damasio, &

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Lee, 1999), and a series of findings demonstrating poor performance on the task after lesion to known emotion-related brain regions such as the ventromesial frontal lobes (Bechara et al., 1994, 1996, 2000, though see also Manes et al., 2002) and amygdala (Bechara et al., 1999).

The Iowa group have argued that the Gambling Task is extremely complex (Damasio, 1994), and that participants do not appear, subjectively, to understand the contingencies of the game (Bechara et al., 1994, 1996, 1997, 2000, though see, Bowman, Evans, & Turnbull, 2005; Evans et al., *in press*; Maia & McClelland, 2004). This has implications for the sorts of memory systems that are available for use when the game is played. Humans typically report relying heavily on explicit episodic memory, which is mediated by hippocampal and related circuits (e.g., Squire, 1992; Tulving & Schacter, 1990). However, Gambling Task findings have demonstrated that complex decision-making may also rely on largely implicit emotion-based learning systems (Bechara et al., 2000, p. 300; cf. Bowman et al., 2005; Evans et al., *in press*). The neurobiology of these systems is less well understood than those mediating episodic memory, but they probably involve the full range of subcortical emotion systems (Berridge, 2003; Cadler, Lawrence, & Young, 2001; Davidson & Irwin, 1999; LeDoux, 2000; Panksepp, 1986, 1998; Patterson & Schmidt, 2003; Phan, Wager, Taylor, & Liberzon, 2002; Rolls, 2000), as well as the connections between these systems and pre-frontal cortex, through the ventromesial frontal lobes (Bechara, 2004; Bechara et al., 2000; Davidson & Irwin, 1999).

It is of especial note that the explicit episodic memory, and emotion-based learning, systems appear to be anatomically independent (Tranel & Damasio, 1993). In principle, therefore, it should be possible to disrupt episodic memory and yet leave emotion-based learning intact. In support of this claim, there have long been reports of intact emotion-based learning in people with amnesia (for review see Eichenbaum & Cohen, 2001). The classic case is that reported by Claparede (1911), who concealed a pin in his palm before shaking the hand of an amnesic patient. On the day following this painful episode, the patient refused to shake the physicians hand, despite having no conscious recollection of the incident (Claparede, 1951). Recent investigations of this phenomenon have been more detailed (e.g., Damasio, Tranel, & Damasio, 1989; Johnson, Kim, & Risse, 1985; Tranel & Damasio, 1990, 1993). For example, Damasio and co-workers described the profoundly amnesic patient, Boswell, who seemed to consistently avoid, or favour, certain hospital staff, though he was unable to explicitly remember the relevant individuals (Tranel & Damasio, 1990, 1993). In a more formal investigation, Boswell was engaged in three types of inter-personal encounter, with individuals who played a 'good', 'neutral' or 'bad' character in all their interactions. At the end of the week Boswell was shown sets of photographs that included the face of one of the individuals, and an unfamiliar face, and was asked to "*Pick the person you would like best?*" (p. 83). Although he had no explicit memory for *any* of

the individuals, Boswell chose the 'good' character some 80% of the time, and almost never chose the bad character (Tranel & Damasio, 1993). Investigations of this type (see also Johnson et al., 1985) suggest that profoundly amnesic patients may retain a capacity to learn emotional valence, demonstrating a single dissociation between emotion-based learning and declarative memory.

However, reports of the sort described above relate to relatively *simple* patterns of emotional valence learning. For example, in the experimental design of the Tranel and Damasio (1993) study, Boswell encountered individuals who were 'good' in *all* of their inter-personal encounters. He was not exposed to the more complex patterns of valence, which characterise everyday life (e.g., Barraclough, Conroy, & Lee, 2004). Here individuals often behave in ways that might be perceived as positive *and* negative on different occasions, though such individuals often can still be judged as 'good' and 'bad' based on some overall, aggregate, assessment of their complex contingency history. It is precisely this complicated pattern of reward and punishment that the Iowa Gambling Task was designed to assess (Bechara et al., 2000).

Of course, this begs the question of what constitutes 'complexity' on tasks of this type. For example, the Wisconsin Card Sorting Task (WCST) is an apparently complex card game, which provides some degree of reward and punishment in its feedback to the patient, through a verbal response (right or wrong) by the examiner. Apparently normal performance in the WCST in amnesia has been reported (e.g., Leng & Parkin, 1988; Moudgil, Azzouz, Al-Azzaz, Haut, & Gutmann, 2000; Shoqirat, Mayes, MacDonald, Meudell, & Pickering, 1990, though see also Squires, Hunkin, & Parkin, 1996; Stefanacci, Buffalo, Schmolck, & Squire, 2000). Similarly, preserved learning in amnesia has been shown on the 'Weather Prediction' task (WPT) that involves the probabilistic predictive power of a series of four cards (Knowlton, Squire, & Gluck, 1994; Knowlton, Mangels, & Squire, 1996). The Iowa Gambling Task (IGT) differs from these measures, as regards apparent 'complexity', in several respects. Firstly, there is the question of the number of 'objects' to be tracked. The IGT involves the tracking of four independent decks of cards, unlike the single deck of the WCST. Also, while the WPT does involve four independent cards, very high performance levels can be achieved by focussing only on a single deck, the most commonly employed strategy (Gluck, Shohamy, & Myers, 2002). Secondly, the IGT repeatedly involves ambiguity of valence: such that a single deck can produce a series of events of randomly-mixed reward and punishment, while the WCST produces consistent reward or punishment when the participant retains a single sorting strategy. Finally, the IGT involves a lengthy series of trials (100), which is far longer than the modified-WCST (48). The WPT *has* been administered for periods over 100 trials (e.g., Gluck et al., 2002) but is notable that the original Knowlton et al.'s (1994, 1996) studies showed that amnesic participants were out-performed by controls after 50 trials, as declarative knowledge became more advantageous for non-amnesics.

Thus, it would be of some interest to observe whether normal Iowa Gambling Task performance can be maintained even in the presence of profound amnesia. The present study demonstrates that it is possible to show normal levels of memory ability on a complex emotion-based learning task, in the presence of profound episodic memory impairment. A patient, SL, who had a dense anterograde amnesia following posterior cerebral artery infarction, was assessed. He performed the Iowa Gambling Task on three occasions, over 3 weeks; and also completed a range of measures of memory and executive abilities. On the Gambling Task he showed normal levels of performance, comparable or better than controls – showing intact complex emotion-based learning – including learning which persisted across substantial periods of time.

1. Case study

1.1. History

SL was an 85-year-old married man, with two grown up children, who worked as a building inspector before he retired. He suffered a posterior cerebral artery stroke in late 2003, 2 months prior to the initial assessment. CT scans indicated a large hypodense area across almost all of the left posterior cerebral artery territory, consistent with a recent infarct (see Fig. 1). On the left side, the lesion involved the medial and lateral surfaces of the occipital lobe, as well as the infero-medial regions of the posterior temporal lobe, including the posterior regions of the hippocampus and the para-hippocampal gyrus. It is not clear whether the damage



Fig. 1. CT scan for SL, showing posterior cerebral artery infarction.

involved regions of the *right* posterior cerebral artery territory that were not visible on scan. However, SL presented with a profound amnesia, and also reported a colour recognition impairment (achromatopsia) in both visual fields, which is consistent with the possibility that both posterior cerebral artery territories were involved.

In spite of his profound amnesia, SL's behaviour towards the investigators appeared to gradually change across sessions (cf. *Tranel & Damasio, 1993, p. 80*). In the earlier sessions, SL appeared to be relatively uncertain about the rationale of his assessment: such as "Who are you?", "Where did you come from?", and "What am I doing?". SL never explicitly recalled who the investigators were, but the uncertainty about people and setting greatly lessened across assessment sessions. Despite never recognising the investigators or the setting in later sessions, he was far more relaxed during assessments, and the repetitive questions about identity and rationale were no longer present.

1.2. Memory

SL displayed marked disorientation for time and place. He knew his name and date of birth, but described his age as 'mid-sixties'. He reported the date as "probably some time in the early 1980's". He was unable to name the current Prime Minister, and guessed it was probably Margaret Thatcher. When asked the age of his children (actually in their forties) SL claimed they were teenagers. He did not recognise any of the regular nursing staff, and could not recall his wife's visits. Even after several visits associated with his neuropsychological assessment, he had no recollection of the examiners, or the different tasks he had performed. Indeed, he did not recall the examiner even when they left the room for a few minutes.

SL's memory and learning abilities were assessed using the Wechsler Memory Scale III (*Wechsler, 1997*):

1.3. Measures of recent episodic memory

Information: 3/18. SL was able to report only his name, date of birth, and mother's first name

Logical Memory: 0/50

Logical Memory Delayed: 0/50

Logical Memory Delayed Recognition: 17/30 (where a chance score is 15/30)

Face Recognition: 23/48 (where a chance score is 24/48)

Face Recognition Delayed: 20/48 (where a chance score is 24/48)

Verbal paired Associates: 0/32

Verbal paired Associates Delayed: 0/8

Verbal paired Associates Delayed Recognition: 20/24 (where a chance score is 12/24)

Family Pictures: 0/64

Family Pictures Delayed: 0/64

Visual Reproduction: 0/104

1.4. Measures of immediate/working memory

Mental Control: 16/16

Digit Span: SL had an audio-verbal span of 7 items forwards, and 2 backwards

Letter-number sequencing: SL had a span of 3 items

Spatial Span: SL had a spatial span of 4 items forwards, and 4 backwards

1.5. Executive functions

Assessment of executive function was limited by SL's achromatopsia (e.g., he could not be tested on the Wisconsin Card Sorting Task, or the Tower of London). However, he did not appear to be impaired on the tests of executive function that he was able to complete (Benton & Hamsher, 1989; Shallice & Evans, 1978; Wilson, Alderman, Burgess, Emslie, & Evans, 1996).

Controlled Oral Word Association Test: total score 31, average

Cognitive Estimates Test: 15/15

Behavioural Assessment of the Dysexecutive Syndrome Rule Shift sub-test: 4/4, average

1.5.1. Comment

SL's performance suggests severe impairments in laying down recent episodic memories, regardless of presentation format. In contrast, he had an immediate memory span within the normal range on a number of tasks, especially on simple measures of audio-verbal recall, such as digit span forwards. One remarkable finding was a surprisingly good performance, well above chance (20/24), in his delayed *recognition* of paired associate items—despite a failure to bring even a single one of the pairs to conscious recall on any of 40 previous exposures to the pairs.

1.6. Iowa Gambling Task

SL completed a version of the Iowa Gambling Task identical to the original Bechara et al. (1994) study. He could choose any card from the four decks (labelled A, B, C, D) in any sequence. Decks A and B were disadvantageous, and C and D advantageous, though the schedule of reward and punishment differed. In Deck A (bad deck) and Deck C (good deck) there were five smaller unpredicted punishments per 10 card selections (thus 20 punishments in total for each deck). On Decks B and D there was only 1 punishment per 10 card selections, which was equal in size to the total 10 card loss on Decks A and C. The only minor difference in administration from that of Bechara et al. was the value of the reward and punishment (see Bowman & Turnbull, 2003). SL was given £2.00 worth of real money, where US\$ 1000 on the Bechara et al. task was equal to £1 in the present study. For the disadvantageous decks (A and B), he won 10p for every card turn, incurring losses of between 15p and £1.25. On the advanta-

geous decks (C and D), SL won 5p for every card turned, incurring losses of between 2p and 25p. He was informed at the start of the game, and regularly throughout the game that he could keep any money they won.

As in Bechara et al. (1994), the task continued until SL had drawn 100 cards. However, it was necessary to explain rules of the task on several occasions, when he asked what task he was performing. SL completed the Gambling Task on three separate sessions, each spaced 1 week apart. In order to counteract any simple effects of learning, such as the fact that Decks C and D were the 'good' decks in the first administration, the contingencies were shifted between sessions. In Session 1, Decks C and D were 'good'; in Session 2, Decks A and D were 'good'; and in Session 3, Decks A and B were 'good' (for more details on the rationale for this shifting pattern see Turnbull et al., *in press*). When first exposed to a task in a given week, SL never recalled performing the task in a previous session.

Four gender and age matched controls (mean age: 81) were recruited through the Bangor University Community Participant Panel. These participants were also tested on the Gambling Task three times, at 1 week intervals. The controls had no history of neurological or psychiatric disorder.

2. Results

Data were analysed in two separate ways: firstly, to observe whether there was learning *during* the individual sessions, and secondly whether there were any cumulative effects of learning *across* sessions.

2.1. Learning during individual sessions

As in Bechara et al. (1994), the 100 card selections were sub-divided into five blocks of 20 trials each. The net score of each block was calculated by subtracting the number of bad from good card selections $[(C+D) - (A+B)]$. A net score above zero implied that the participants were selecting cards advantageously. For the purposes of this investigation, the control participants and SL's performance was averaged across each of the three sessions.

There was a progressive increase, across blocks, in advantageous card selections for both SL and the control participants (see Fig. 2). Performance levels began close to chance, and increased to levels substantially above chance by Block 5. Single case study *t*-tests (see Crawford & Garthwaite, 2002, for further detail) were employed to investigate a possible difference between SL and the controls performance on the Gambling Task (averaged across the three sessions). There were no significant differences between SL and controls' performance in four of the five blocks (*t*-values ranging from 0.20 to 0.53, all significance levels $p > 0.05$). SL's performance was significantly *better* than controls in block 2 ($t = 3.71$, $p < 0.05$).

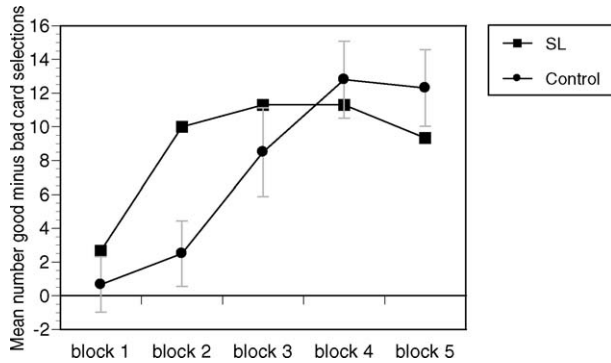


Fig. 2. Performance of SL and controls on the Iowa Gambling Task, averaged across three sessions.

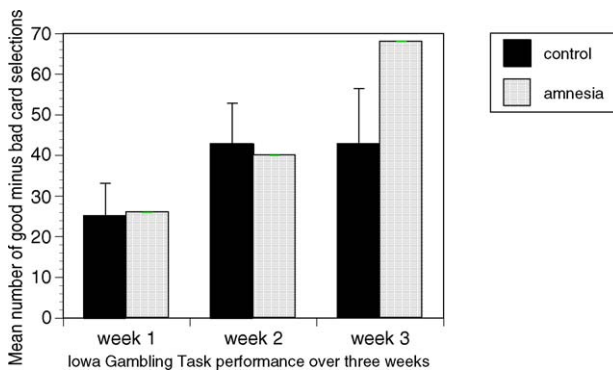


Fig. 3. Performance of SL and controls on the Iowa Gambling Task, averaged across block, over three sessions.

2.2. Cumulative effects of learning across sessions

To investigate performance over the three sessions, a net score for the entire task was calculated by subtracting the number of good from bad card selections $[(C + D) - (A + B)]$ for all 100 trials. Again, a net score above zero implied that the participants were selecting cards advantageously.

There was a progressive increase in advantageous card selections across sessions (see Fig. 3) for both SL and the controls. Again, *t*-tests revealed no significant difference between SL and controls' performance in any session (Session 1 ($t = 0.06$, $p = 0.48$); Session 2 ($t = -0.12$, $p = 0.46$); Session 3 ($t = 0.83$, $p = 0.24$)). Notably, however, SL performed (non-significantly) *better* than controls in Session 3.

3. Discussion

The key aim of the present study was to evaluate the performance of an amnesic patient on a measure of complex emotion-based learning. SL presented with a profound impairment of recent episodic memory, as shown by a range of floor, or chance, performances. In contrast, he showed reasonable levels of performance on tasks of immediate/working memory. This pattern of performance is entirely consistent with the sorts of episodic amnesia typically

observed after lesion to the hippocampal memory system (Squire, 1992).

However, in striking contrast to his poor performance on tasks of recent episodic memory, SL showed apparently normal levels of performance on the Iowa Gambling Task, even out-performing age-matched controls on some blocks. This learning took place despite SL being unable to recall the rules of the task for more than a few consecutive trials, and being unable to recall anything of the task directly after performing it. While preserved learning on card game tasks has been reported before in amnesia (e.g., Knowlton et al., 1994, 1996; Leng & Parkin, 1988; Moudgil et al., 2000; Shoqeirat et al., 1990), the preserved learning in SL is reported on a task that is (as mentioned in the Introduction) notably more complex than those previously employed: in terms of number of independent decks, number of trials, and most importantly because of ambiguity of valence.

This latter finding, of entirely normal levels of performance on a 100 trial task, is especially striking given that the Knowlton et al. 'Weather Prediction' studies (1994, 1996) showed that amnesic participants were eventually outperformed by controls after 50 trials, presumably because declarative knowledge became more advantageous. However, the Iowa Gambling Task has a more explicit regime of reward and punishment (winning and losing real money) than the 'Weather Prediction' task, and it may be that an amnesic such as SL is better able to capitalise on more powerfully experienced emotion-based knowledge. Indeed, SL appeared to perform at even *higher* levels than controls in the later blocks, after more than 200 trials. This may be because controls attempt to solve the Iowa Gambling Task by using explicit conceptual strategies, not available to SL, though such approaches may be counter-productive (Evans, Kemish, & Turnbull, 2004).

SL was also able to demonstrate a regular and systematic improvement in performance over three test sessions, each separated by 1 week: where his performance was comparable, or better, than controls. This improvement occurred despite the fact that the reward-contingency pattern was shifted between sessions, and that SL was unable to explicitly recall any aspect of his performance in the previous sessions, or even to recognise the examiner. This ability to retain and build on established emotion-based knowledge, across long periods of time, suggests that these memory systems have substantial levels of temporal stability, with some additional capacity for flexibility.

One especially interesting finding was a remarkably good performance, well above chance levels, in SL's *recognition* of paired-associate items. He had comprehensively failed to bring even a single one of these pairs to conscious recall on any his 40 previous exposures to the pairs, but nevertheless appeared to have encoded at least some aspect of a memorial linkage between them. One possibility is that he had stored some emotional marker associated with each pair ('rose-bag', *good*; 'elephant-glass', *bad*). Another possibility is that the previously tested items had acquired some pos-

itive emotional valence through the ‘mere-exposure’ effect (Zajonc, 1980). These arguments remain speculative, but clearly this finding bears on the important question of how episodic memory abilities are bolstered by additional resources from other memory systems, and this issue merits replication and further investigation in other amnesic patients.

These findings support the consensus that there are multiple memory systems in the brain, each with functionally and anatomically distinct neural substrates, especially supporting an anatomical and functional dissociation between episodic and emotion-based memory. Importantly, the emotion-based learning systems appear able to encode more sophisticated patterns of valence learning than have previously been reported, and sustain these over substantial periods of time. However, to further investigate this topic, it will be of some interest to assess a range of amnesic individuals, for example, establishing whether such learning is universally found in amnesic patients, and whether the effect can be found after amnesia of the ‘diencephalic’ sub-type, in addition to those with ‘hippocampal’ amnesia.

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References

- Barraclough, D. J., Conroy, M. L., & Lee, D. (2004). Prefrontal cortex and decision-making in a mixed-strategy game. *Nature Neuroscience*, 7, 404–410.
- Bechara, A. (2004). A neural view of the regulation of complex cognitive functions by emotion. In P. Philippot & R. S. Feldman (Eds.), *The regulation of emotion*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision-making and the orbitofrontal cortex. *Cerebral Cortex*, 10, 295–307.
- Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to prefrontal cortex. *Cognition*, 50, 7–15.
- Bechara, A., Damasio, H., Damasio, A. R., & Lee, G. P. (1999). Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. *The Journal of Neuroscience*, 19(13), 5473–5481.
- Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science*, 275, 1293–1294.
- Bechara, A., Tranel, D., Damasio, H., & Damasio, A. R. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, 6, 215–225.
- Benton, A. L., & Hamsher, K. (1989). *Multilingual aphasia examination*. Iowa City, IA: AJA Associates.
- Berridge, K. C. (2003). Pleasures of the brain. *Brain and Cognition*, 52, 106–128.
- Bickel, W. K., Degrandpre, R. J., & Higgins, S. Y. (1995). The behavioural economics of concurrent drug reinforcers—A review and reanalysis of drug self-administration research. *Psychopharmacology*, 118, 250–259.
- Bowman, C. H., & Turnbull, O. H. (2003). Real versus facsimile reinforcers on the Iowa Gambling Task. *Brain & Cognition*, 53, 207–210.
- Bowman, C. H., & Turnbull, O. H. (2004). Emotion-based learning on a simplified card task: The Iowa and Bangor Gambling Tasks. *Brain and Cognition*, 55, 277–282.
- Bowman, C. H., Evans, C. E. Y., & Turnbull, O. H. (2005). Artificial time-constraints on the Iowa Gambling Task: The effects on behavioural performance and subjective experience. *Brain and Cognition*, 57, 21–25.
- Cadler, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nature Reviews*, 2, 352–363.
- Claparede, E. (1951). Recognition and “me”ness. In D. Rapaport (Ed.), *Organisation and pathology of thought* (pp. 58–75). New York: Columbia University Press (Reprinted from *Archives de Psychologies*, 11, 79–90 (1911)).
- Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, 40, 1196–1208.
- Damasio, A. R. (1994). *Descartes’ error: Emotion, reason, and the human brain*. New York: Putnam.
- Damasio, A. R. (1996). *The somatic marker hypothesis and the possible functions of the prefrontal cortex: Vol. B351*. London: Philosophical Transactions of the Royal Society, pp. 1413–1420.
- Damasio, A. R., Tranel, D., & Damasio, H. (1989). Amnesia caused by herpes simplex encephalitis, infarctions in basal forebrain, Alzheimer’s disease, and anoxia. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology: Vol. 3*. Amsterdam: Elsevier, pp. 149–166.
- Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, 3, 11–21.
- Eichenbaum, H., & Cohen, N. J. (2001). *From conditioning to conscious recollection: Memory systems of the brain*. Oxford: Oxford University Press.
- Evans, C. E. Y., Bowman, C. H., & Turnbull, O. H. Subjective awareness on the Iowa Gambling Task: The key role of emotional experience in schizophrenia. *Journal of Clinical and Experimental Neuropsychology*, in press.
- Evans, C. E. Y., Kemish, K., & Turnbull, O. H. (2004). Paradoxical effects of education on the Iowa Gambling Task. *Brain & Cognition*, 54, 240–244.
- Gluck, M. A., Shohamy, D., & Myers, C. (2002). How do people solve the ‘Weather Prediction’ task? Individual variability in strategies for probabilistic category learning. *Learning & Memory*, 9, 408–418.
- Johnson, M. H., Kim, J. K., & Risse, G. (1985). Do alcoholic Korsakoff’s syndrome patients acquire affective reactions? *Journal of Experimental Psychology: Learning Memory and Cognition*, 11, 27–36.
- Knowlton, B., Squire, L. R., & Gluck, M. (1994). Probabilistic classification learning in amnesia. *Learning and Memory*, 1, 106–120.
- Knowlton, B., Mangels, J., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science*, 273, 1399–1402.
- LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, 23, 155–184.
- Leng, N. R., & Parkin, A. J. (1988). Double dissociation of frontal dysfunction in organic amnesia. *British Journal of Clinical Psychology*, 27, 359–62.
- Manes, F., Sahakian, B., Clark, L., Rogers, R., Antonin, N., Aitken, M., et al. (2002). Decision-making processes following damage to the prefrontal cortex. *Brain*, 125, 624–639.
- Maia, T. V., & McClelland, J. L. (2004). A re-examination of the evidence for the somatic marker hypothesis: What participants really know in the Iowa Gambling task. *Proceedings of the National Academy of Sciences*, 101, 16075–16080.

- Moudgil, S. S., Azzouz, M., Al-Azzaz, A., Haut, M., & Gutmann, L. (2000). Amnesia due to fornix infarction. *Stroke*, *31*, 1418.
- Panksepp, J. (1986). The anatomy of emotions. In R. Plutchik & H. Kellerman (Eds.), *Biological foundations of emotions: Vol. 3. Emotion, theory, research and experience*. Academic Press.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human emotions*. Oxford: Oxford University Press.
- Patterson, D. W., & Schmidt, L. A. (2003). Neuroanatomy of the human affective system. *Brain and Cognition*, *52*, 24–26.
- Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage*, *16*, 331–348.
- Rogers, R. D., Owen, A. M., Middleton, H. C., Williams, E. J., Pickard, J. D., Sahakian, B. J., et al. (1999). Choosing between small, likely rewards and large, unlikely rewards activates inferior and orbital prefrontal cortex. *The Journal of Neuroscience*, *20*(19), 9029–9038.
- Rolls, E. T. (2000). Precis of the brain and emotion. *Behavioural and Brain Sciences*, *23*, 177–234.
- Rolls, E. T., Hornack, J., Wade, D., & McGrath, J. (1994). Emotion related learning in patients with social and emotional changes associated with frontal lobe damage. *Journal of Neurology, Neurosurgery and Psychiatry*, *57*, 1518–1524.
- Shallice, T., & Evans, M. E. (1978). The involvement of the frontal lobes in cognitive estimation. *Cortex*, *14*, 294–303.
- Shoqeirat, M. A., Mayes, A., MacDonald, C., Meudell, P., & Pickering, A. (1990). Performance on tests sensitive to frontal lobe lesions by patients with organic amnesia: Leng & Parkin revisited. *British Journal of Clinical Psychology*, *29*, 401–408.
- Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*, 195–231.
- Squires, E. J., Hunkin, N. M., & Parkin, A. J. (1996). Memory notebook training in a case of severe amnesia. *Neuropsychological Rehabilitation*, *6*, 55–66.
- Stefanacci, L., Buffalo, E. A., Schmolck, H., & Squire, L. R. (2000). Profound amnesia after damage to the medial temporal lobe: A neuroanatomical and neuropsychological profile of patient E.P. *The Journal of Neuroscience*, *20*, 7024–7036.
- Tomb, I., Hauser, M., Deldin, P., & Caramazza, A. (2002). Do somatic markers mediate decisions on the gambling task? *Nature Neuroscience*, *14*, 1099–1108.
- Turnbull, O. H., Berry, H., & Bowman, C. H. (2003). Direct versus indirect emotional consequences on the Iowa Gambling Task. *Brain and Cognition*, *53*, 389–392.
- Turnbull O. H., Evans C. E. Y., Kemish K., Park S., Bowman C. H. (in press). A novel 'set-shifting' modification of the Iowa Gambling Task: Flexible emotion-based learning in schizophrenia. *Neuropsychology*.
- Tranel, D., & Damasio, A. R. (1990). Covert learning of emotional valence in patient Boswell. *Journal of Clinical Psychology and Experimental Neuropsychology*, *12*, 27.
- Tranel, D., & Damasio, A. R. (1993). The covert learning of affective valence does not require structures in hippocampal system or amygdala. *Journal of Cognitive Neuroscience*, *5*(1), 79–88.
- Tulving, E., & Schacter, D. (1990). Priming and human memory systems. *Science*, *247*, 301–306.
- Wilson, B. A., Alderman, N., Burgess, P., Emslie, H., & Evans, J. J. (1996). *Behavioural assessment of the dysexecutive syndrome*. Thames Valley Test Company.
- Wechsler, D. (1997). *Wechsler Memory Scale* (3rd ed.). San Antonio, TX: The Psychological Corporation.
- Zajonc, R. B. (1980). Feeling and thinking: Preferences need no inferences. *American Psychologist*, *35*, 547–563.