

BRIEF REPORTS

When Side Matters: Hemispheric Processing and the Visual Specificity of Emotional Memories

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Previous studies have shown that the right hemisphere processes the visual details of objects and the emotionality of information. These two roles of the right hemisphere have not been examined concurrently. In the present study, the authors examined whether right hemisphere processing would lead to particularly good memory for the visual details of emotional stimuli. Participants viewed positive, negative, and neutral objects, displayed to the left or right of a fixation cross. Later, participants performed a recognition task in which they evaluated whether items were “same” (same visual details), “similar” (same verbal label, different visual details), or “new” (unrelated) in comparison with the studied objects. Participants remembered the visual details of negative items well, and this advantage in memory specificity was particularly pronounced when the items had been presented directly to the right hemisphere (i.e., to the left of the fixation cross). These results suggest that there is an episodic memory benefit conveyed when negative items are presented directly to the right hemisphere, likely because of the specialization of the right hemisphere for processing both visual detail and negatively valenced emotional information.

Keywords: emotion, hemisphere, laterality, memory, visual field

We sometimes remember information with tremendous visual specificity. Yet at other times our memories can lack visual details. We may be able to describe in perfect detail the dress that our favorite movie star wore to the Oscars, but we may have no idea what our professor was wearing at this morning’s meeting.

When it comes to remembering the precise visual details of an object, it is believed that the right hemisphere (RH) may play a particularly important role. Kosslyn and colleagues have proposed that coordinate-based visuospatial processing, including the spatial relationships between objects or among an object’s features, may preferentially occur in the RH, whereas categorical-based processing may arise through left hemisphere (LH) involvement (Kosslyn, 1987; Kosslyn et al., 1989). Marsolek and colleagues have similarly proposed that processing of specific exemplars may operate more efficiently in the RH, whereas processing of abstract categories may occur more effectively in the LH (e.g., Burgund & Marsolek, 2000; Marsolek, 1995, 1999).

In support of a distinction between the processing that occurs in the RH and LH, a number of studies have revealed that memory for

item-specific information can be improved when stimuli are presented to the left visual field (LVF) and thus processed by the RH. By contrast, reliance on abstract or heuristic information can be enhanced when information is presented in the right visual field (RVF) and thus processed directly by the LH (Marsolek, 1995, 1999; Marsolek & Burgund, 2008; Marsolek, Schacter, & Nichols, 1996; Marsolek, Squire, Kosslyn, & Lulenski, 1994). Within the realm of object processing, neuroimaging studies have suggested that the fusiform gyrus, in particular, may process information differently depending upon the hemisphere. The right fusiform gyrus responds strongly to item-specific attributes, such as an object’s size, color, shape, or orientation, whereas the left fusiform gyrus responds more generally to global item features. Thus, the right fusiform gyrus shows robust habituation if the same exemplar of an item is shown repeatedly (e.g., if the same kitten is shown multiple times), but it shows little habituation if different exemplars of the same type of item are shown repeatedly (e.g., if different kittens are shown). By contrast, the left fusiform gyrus shows significant habituation even when different exemplars are repeated (Koutstaal et al., 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003). Activity in the right fusiform gyrus also shows a strong correspondence to a person’s ability to remember the precise visual details of an object, whereas activity in the left fusiform gyrus relates to later memory for the general object type but not for the object’s visual details (Garoff, Slotnick, & Schacter, 2005; Kensinger, Garoff-Eaton, & Schacter, 2007c).

A separate literature has suggested that the RH may be specialized not only for processing specific object representations but also for processing emotional—and perhaps specifically negative—information (reviewed by Borod, 1992; Davidson, 1992;

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Kucharska-Pietura, 2006). For example, patients with brain damage in the LH (but a preserved RH) are more likely to dwell on negative information and to suffer from depressive symptoms, whereas patients with brain damage in the RH are more likely to display a shift away from the negative, sometimes displaying mania (e.g., Lee, Loring, Meader, & Brooks, 1990; Morris et al., 1996; Paradiso et al., 1999; Sackeim et al., 1982; Starkstein et al., 1989). Distinctions between LH and RH processing of emotional information also are readily apparent in healthy individuals. If a chimeric face is presented to a participant, with the left half of the face (presented to the RH) displaying one expression and the right half of the face (presented to the LH) displaying another expression, participants will be more likely to label the expression presented to the RH (see recent review by Bourne, 2008). Affective priming also is more likely to occur when stimuli are presented to the LVF/RH than when they are presented to the RVF/LH (Sato & Aoki, 2006; see also Collins & Cooke, 2005, for evidence that priming for emotional information can be greater following RH processing). Though many theories regarding the hemispheric processing of emotion processing have focused on laterality differences within the prefrontal cortex (Davidson, 1995; Davidson & Irwin, 1999), it also has been proposed that the right visual cortex is more sensitive to emotional stimuli than the left visual cortex, perhaps because of strong connections between the right amygdala and the right visual cortex (Landis, 2006).

Though a few studies have indicated that implicit memory for emotional items can vary as a function of hemispheric presentation, the present study asked whether this overlap in RH specialization for processing both the visual details of objects and the emotional content of information would lead to a benefit in *episodic* memory. In particular, we examined whether memory for the visual details of emotional items would be enhanced when those items were presented to the LVF/RH. It has previously been shown that negative items are more likely than neutral ones to be remembered with specific visual details but that such benefits occur only with sufficiently long presentation durations (Kensinger, Garoff-Eaton, & Schacter, 2006). The present experiment examined whether benefits in remembering the specific visual details of negative items would occur even when items were presented briefly, if those items were presented directly to the RH (via LVF presentation).

Method

Participants

Participants were 26 Boston College undergraduate and graduate students (18 men and 8 women; mean years of education = 13.5 years) between the ages of 18 and 26 years (mean age = 19.5 years). Participants were native English speakers with normal or corrected-to-normal vision. No participant reported taking any medication that affected the central nervous system. No participant reported a history of depression or other psychiatric illness or any neurological disorder. All participants reported that they were right-handed, and handedness was assessed via the Edinburgh Handedness Inventory (Oldfield, 1971). This inventory asks whether participants have a strong or weak handedness preference when performing a series of activities (writing, drawing, throwing, striking match, opening box lid, and holding scissors, toothbrush, knife, spoon, or broom handle). Scores for each activity range from

1 (*always use left hand*) to 5 (*always use right hand*). This inventory confirmed that all of our participants were strongly right-handed ($M = 4.5$, $SE = 0.06$). Informed consent was obtained from all participants in a manner approved by the Boston College Institutional Review Board.

Materials

Materials comprised 180 pairs of photo objects (from Kensinger et al., 2007b, 2007c). Pairs shared the same verbal label (e.g., were both canoes) but differed in other perceptual features (e.g., color, shape, size, orientation). The pairs were selected from a larger set that had been rated for valence and arousal by a separate group of adults. One third of the selected objects were negative and arousing (i.e., valence ratings less than 3.5 on a 9-point Likert scale, with low numbers signifying negative valence; arousal ratings greater than 5 on a 9-point Likert scale), one third were positive and arousing (i.e., valence ratings greater than 5.5 and arousal ratings greater than 5), and one third were neutral (i.e., valence ratings between 3.5 and 5.5 and arousal ratings less than 5). The positive and negative objects did not differ from one another in arousal or in absolute valence (i.e., distance from a neutral valence rating of 5; $ps > .15$), and positive and negative objects were significantly more arousing than neutral ones ($p < .001$).

Pairs also had been rated for the overall similarity of the two items, the dimensions (color, size, shape, orientation) that differed between the two items, and the familiarity of the items (see Kensinger et al., 2006, for details of matching procedures). Negative, positive, and neutral pairs were carefully matched on each of these dimensions ($ps > .15$). In particular, negative, positive, and neutral objects were selected to be similar in visual complexity and to be from the same types of categories (e.g., included approximately the same number of animals, manmade objects, foods). We also examined the word frequencies for the object names (as reported by Coltheart, 1981) and selected items so that there were no differences in word frequency across the three categories of emotional items.

Procedure

During the study phase, participants were asked to view a series of 144 objects (one third of each emotional valence) while their eyes remained focused on a dark fixation cross in the center of the computer screen. Each object was presented for 250 ms, and there was a 3,750-ms interstimulus interval. Half of the objects from each emotional valence category were presented to the left of the fixation cross and half were presented to the right of the cross. So that objects were presented directly to only one hemisphere, the center of each object was presented approximately 7° to the left or right of the fixation cross. The order of the presented items was randomized for each odd-numbered participant; the even-numbered participants saw the same items, in the same order as the previous participant, but each item was presented in the opposite hemifield (e.g., if Participant 1 saw a canoe presented in the LVF followed by a grenade presented in the RVF, then Participant 2 saw a canoe presented in the RVF followed by a grenade presented in the LVF).

To ensure that participants were attending to each object, after each object was presented and during the interstimulus interval, we instructed participants to press one key to indicate that the object

would fit inside a file cabinet drawer or a different key to indicate that the object was too big to fit. This task was selected because answering it required that participants had processed the object, but the task did not require participants to attend to the precise visual details of the objects or to the emotional significance of the objects. To avoid fatigue, participants were given short breaks approximately every 2.5 min. When a “Get Ready” prompt appeared on-screen, participants made a mouse-click when they were ready to continue the task.

Immediately following completion of the study phase, participants were asked to perform a surprise recognition memory task. Participants had believed that the purpose of the study phase was to assess how hemispheric presentation influenced the speed with which decisions could be made about objects, and so participants were not expecting that their memory for these objects would be tested. Debriefing forms confirmed that the incidental encoding manipulation was successful; no participant reported that he or she had thought that the experiment would assess memory for the objects.

On the recognition memory task, participants were once again asked to view a series of objects presented on-screen. This time each of 180 objects was presented in the center of the screen. Of the 180 objects, 72 (24 negative, 24 positive, 24 neutral) were the identical object that had been studied (e.g., the *same* canoe), 72 shared the same verbal label as a studied object but differed in visual details (e.g., a *similar* snake), and 36 (12 of each emotional valence) did not share a verbal label with a presented object (e.g., a *new* hammer; see Kensinger et al., 2006, for more information on these methods). Participants were instructed to indicate, by button press, whether the picture was “same” (identical), “similar,” or “new,” in relation to the previous study list.

Only one object within the object pair was tested across all participants (i.e., participants never saw both a *same* and a *similar* snake). The same recognition task was given to all participants. The studied items were counterbalanced between subjects to manipulate the condition of each object shown at recognition (i.e., whether it was *same*, *similar*, or *new*) and on the side of the screen on which the item had been studied.

A pilot sample of participants was tested while eye-tracking patterns were recorded during the study phase, to ensure that participants could maintain fixation on the central point. The behavioral data from these participants, during both study and test phases, paralleled the data from those participants whose eye gaze was not objectively measured. These pilot participants made only a small number of fixation errors (less than 3% of all trials), and errors did not differ as a function of hemispheric presentation or emotional valence category. Thus, we have no reason to believe that the participants in the present study were unable to fixate on the cross during the study phase.¹

Data Analysis

We focused our analyses on three types of memory that have been defined previously using this paradigm (Kensinger, Garoff-Eaton, & Schacter, 2007a; Payne, Stickgold, Swanberg, & Kensinger, in press): *general recognition* memory, or memory for at least the gist of the items, with or without memory for visual detail; memory for *specific visual detail*; and *gist-only memory*, lacking in

visual detail. For general recognition memory, we computed d' sensitivity measures (Snodgrass & Corwin, 1988), considering “same” or “similar” responses to *same* or *similar* items to reflect general recognition hits and considering “same” or “similar” responses to *new* items to reflect general false-alarm responses. That is, for *same* and *similar* items given either a “same” or a “similar” response, participants had to remember at least that a particular type of object had been studied (e.g., that they had seen a canoe) because otherwise they would have indicated that the item was “new.” Thus, these general recognition scores reflect a participant’s tendency to remember at least the gist of the items (with or without visual detail). By contrast, when participants gave a “same” or “similar” response to a *new* item, these responses reflected false alarms, revealing a participant’s bias to indicate that a general item type had been studied. Because by definition the *new* items were not studied, there was only one false-alarm rate (it did not vary on the basis of hemispheric presentation). We calculated d' scores as recommended by Snodgrass and Corwin (1988) using these hit and false-alarm rates.

For visually specific recognition memory, we examined what proportion of the *same* items for which general recognition occurred (i.e., for which “same” or “similar” responses were given) were also associated with specific recognition (i.e., a “same” response to a *same* item).² These proportional scores, reflecting specific recognition hits, were calculated as follows: “same” responses to *same* items/ (“same” + “similar” responses to *same* items). Specific recognition false alarms, reflecting participants’ tendencies to say incorrectly that a familiar item was “same,” were considered to be the comparable proportion for *similar* items: “same” responses to *similar* items/ (“same” + “similar” responses to *similar* items). Though *similar* items had not been studied, we considered a *similar* item to be associated with RVF/LH presentation if its corresponding object had been studied in that condition (e.g., if Penguin A was studied in the RVF/LH condition, then Penguin B was considered to be a *similar* object associated with RVF/LH presentation). We computed d' measures of sensitivity (Snodgrass & Corwin, 1988) using these hit and false-alarm rates. Please see Table 1 for raw response rates that were used to calculate these scores.

For gist-only memory, we considered “similar” responses to *same* items to reflect gist-only hits and “similar” responses to *new* items to reflect gist-only false alarms. Using these computations, we calculated d' sensitivity values. Because by definition the *new* items were not studied, there was only one false-alarm rate (it did not vary on the basis of hemispheric presentation).

¹ We did not perform eye tracking with the participants in this experiment because we were concerned that the novel and somewhat stressful eye-tracking environment might induce mood effects that could influence our results.

² Note that responses to *similar* items are harder to interpret with regard to memory specificity. A “similar” response to a *similar* item could reflect memory for specific details (e.g., maybe participants give a “similar” response to a *similar* snake because they remember the exact snake they studied and know that this is not that same snake). However, a “similar” response to a *similar* item also might reflect memory for only the gist of an item (e.g., maybe a person does not remember what the snake looked like and so claims this is a “similar” one).

Table 1
Proportion of Responses Given to Objects as a Function of Object Type, Emotion Type, and Hemispheric Presentation

Response type	Same item					
	Negative emotion		Positive emotion		Neutral emotion	
	LVF/RH	RVF/LH	LVF/RH	RVF/LH	LVF/RH	RVF/LH
Same	.63 (.04)	.46 (.04)	.44 (.04)	.41 (.05)	.42 (.04)	.39 (.03)
Similar	.15 (.02)	.27 (.02)	.27 (.03)	.32 (.02)	.23 (.03)	.26 (.02)
New	.22 (.03)	.27 (.03)	.29 (.04)	.27 (.04)	.34 (.05)	.34 (.04)
	Similar item					
Same	.14 (.02)	.15 (.02)	.12 (.02)	.10 (.03)	.13 (.02)	.12 (.04)
Similar	.52 (.03)	.50 (.03)	.46 (.05)	.40 (.05)	.42 (.04)	.44 (.04)
New	.33 (.04)	.35 (.03)	.43 (.05)	.50 (.05)	.45 (.05)	.44 (.05)
	New item ^a					
Same		.03 (.01)		.01 (.01)		.02 (.01)
Similar		.18 (.03)		.10 (.01)		.16 (.02)
New		.78 (.03)		.89 (.01)		.82 (.02)

Note. Values in parentheses represent standard error of the mean. LVF = left visual field; RVF = right visual field; LH = left hemisphere; RH = right hemisphere.
^a Because *new* items were presented only at test, they are not associated with a hemispheric presentation at study.

We also computed response bias measurements for each of the memory measures described above. Because these measurements were never influenced by hemispheric presentation (i.e., analyses of variance [ANOVAs] revealed no main effects of hemisphere presentation or any interactions between emotional valence and hemisphere), we do not report these analyses.

Results

General Recognition

An ANOVA conducted on the general recognition d' values with emotional valence (positive, negative, neutral) and hemispheric presentation (left, right) as within-subject factors indicated only a main effect of emotion, $F(2, 50) = 3.47, p < .05, \eta_p^2 = .12$, with negative and positive items having higher general recognition than neutral items. The hemisphere of presentation did not influence general recognition ability ($p > .25$), nor did the interaction between the two factors.

Memory for Specific Visual Detail

An ANOVA conducted on the specific recognition d' scores revealed a main effect of hemispheric presentation, $F(1, 25) = 4.29, p < .05, \eta_p^2 = .18$, with items presented directly to the LVF/RH remembered with better specificity than items presented to the RVF/LH. The ANOVA also revealed an interaction between hemispheric presentation and emotional valence, $F(2, 50) = 3.30, p < .05, \eta_p^2 = .12$. As can be seen in Figure 1, this interaction reflected the fact that specific recognition was highest when items were negative and presented in the LVF. In fact, the benefit of negative emotion on memory specificity existed when negative items were presented only in the LVF ($p < .001$) and not in the RVF ($p > .15$).

Gist-Only Memory

An ANOVA conducted on the gist-only d' scores revealed a main effect of emotional valence, $F(2, 50) = 13.39, p < .001$,

$\eta_p^2 = .35$, with positive items more likely to be remembered with gist-only information than with negative or neutral items, and a main effect of hemispheric presentation, $F(1, 25) = 17.28, p < .001, \eta_p^2 = .41$, with items presented in the right hemifield (i.e., directly to the LH) more likely to be remembered with gist-only information (see Figure 2). There was no interaction between the two factors ($p > .25$).

Discussion

The present results provide strong evidence for a unique memory benefit when items are negative and presented directly to the RH (via LVF presentation). In this instance, even with brief presentation, episodic memory for the visual details of negative items is enhanced. By contrast, when the items are presented briefly and directly to the LH (via RVF presentation) or are presented briefly in the center of the screen (Kensinger et al., 2006), no such memory benefits exist.

Given the proposed role of the RH in processing the visual specifics or relational details of objects, and in processing emotional and perhaps particularly negative information, it makes sense that LVF/RH processing would lead to enhanced memory for the visual details of negative items. Nevertheless, this is one of the few studies to show such an effect of hemispheric processing on episodic encoding for objects (but see Berrini, Della Sala, Spinnler, Sterzi, & Vallar, 1982; Evans & Federmeier, 2007; Federmeier & Benjamin, 2005; Hannay & Malone, 1976, for evidence that hemifield presentation can influence subsequent episodic memory for words) and the first to show that the magnitude of the emotion-related enhancement in episodic memory can be modulated by hemifield presentation. Thus, these results are intriguing in suggesting that the magnitude of memory benefit conveyed by emotional information may vary depending upon which hemisphere first processes information. The enhancement in memory specificity for negative information is greatest when the RH receives high-fidelity information rapidly. This finding is broadly consistent with recent neuroimaging evidence suggesting that when the right fusiform and right amygdala are engaged during encoding,

Specific Recognition Memory for Visual Detail

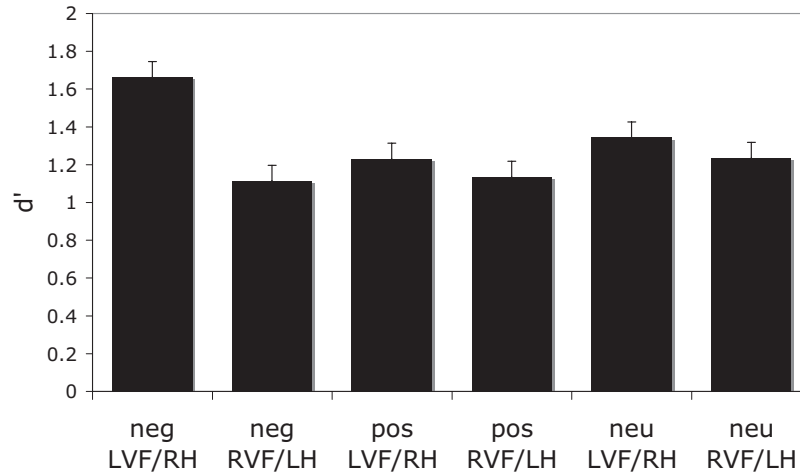


Figure 1. When items were presented directly to the left visual field or to the right hemisphere (LVF/RH), participants were more likely to remember the visual details of negative (neg) items than they were to remember the visual details of positive (pos) or neutral (neu) items. No such advantage existed when items were presented directly to the right visual field or to the left hemisphere (RVF/LH). Error bars represent standard error of the mean.

negative items are particularly likely to be remembered with specific visual detail (Kensinger et al., 2007c). The present results suggest that this right-lateralized processing may be facilitated by giving the RH a “head start” in processing the information.

More broadly, the results of the present study further support a distinction between the types of processing mediated by the LH and RH. In the present study, when information was presented

directly to the LVF/RH, memory for specific visual detail was enhanced, whereas when information was presented directly to the RVF/LH, information was more likely to be remembered with gist-only information. This pattern of results is consistent with the proposal that the RH is specialized for processing the visual specifics or relational details of objects, whereas the LH is recruited for the processing of more general or conceptual features of

Gist-Only Memory

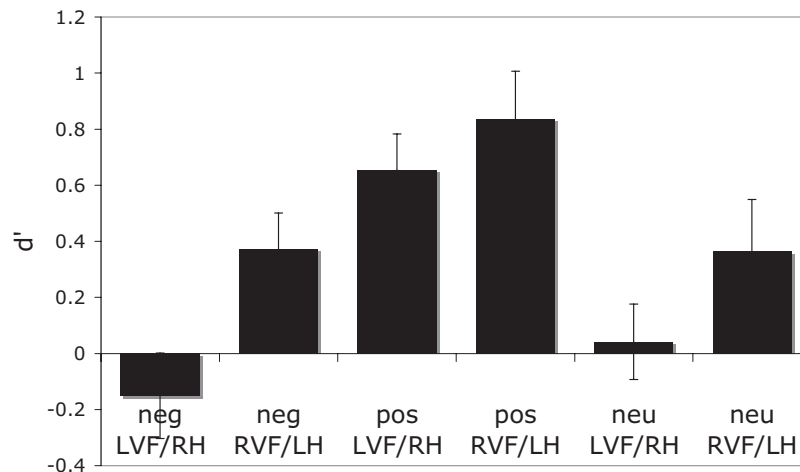


Figure 2. Gist-only information was more likely to be remembered when items had been presented directly to the right visual field or the left hemisphere (RVF/LH) than when they had been presented directly to the left visual field or the right hemisphere (LVF/RH). The low d' values for negative (neg) and neutral (neu) items suggest that participants rarely remembered the gist of those items without their specific visual details, whereas this gist-only recognition occurred more reliably for positive (pos) items. Error bars represent standard error of the mean.

objects (e.g., Burgund & Marsolek, 2000; Kosslyn, 1987; Kosslyn et al., 1989; Marsolek, 1995, 1999). This finding is also consistent with recent event-related potential evidence that the neural processes involved in determining whether a test item is a perceptual match to a studied item are more likely to be involved if the item was studied in the LVF/RH than if it was studied in the RVF/LH (Evans & Federmeier, 2007). Taken together with the results of the present study, these results provide convincing evidence that RH processing can lead to better retention of the details of studied information, making it easier to determine whether another item is a perceptual match to that studied item.

The fact that the effects of RH presentation on memory for visual specificity interacted with emotion but the effects of LH presentation on memory for gist-only information did not, may reflect the lack of specialized emotional processing in the LH. As outlined in the introduction, many lines of evidence suggest that the RH may play a particularly important role in processing information with emotional meaning (e.g., Bourne, 2008). However, it also has been proposed that there are valence-specific effects, with the RH specialized for processing negative emotion and the LH optimized for processing positive emotion (e.g., Davidson, 1995; Natale, Gur, & Gur, 1983; Sackeim et al., 1982; Schaffer, Davidson, & Saron, 1983). If the latter hypothesis were true, then it might be expected that there should be an interaction between emotion and subsequent memory in the LH as well, with the gist of positive items being more likely to be remembered when they are presented directly to the LH. At the present time, it is unclear whether our measure of gist-only recognition is insufficiently sensitive to detect interactions with emotion or whether no such interactions exist. It will be important for future studies to examine whether there can be interactions between emotional valence and subsequent episodic memory performance when information is presented directly to the LH.

There are a few limitations of the present study that should be noted. First, these findings are based upon a small sample drawn from a college campus, preventing us from examining whether the effects vary with age, gender, or other individual differences. Second, we saw only modest effects of direct hemispheric presentation on memory for neutral items (see Figure 1), though such an effect would be hypothesized to occur due to the RH role in processing exemplar-specific details. It is possible that the parameters of this study (e.g., stimulus presentation duration, encoding task, study–test delay) were not optimal for detecting the effects of direct hemispheric presentation on memory for neutral items. Alternatively, it is possible that intermixing negative, positive, and neutral items changes the way in which neutral information is attended and processed (see Grünh, Scheibe, & Baltes, 2007; Strange, Henson, Friston, & Dolan, 2000, for evidence), reducing the link between direct RH presentation and encoding of specific visual details. Future studies comparing mixed lists to blocked lists could address this possibility. More generally, future research will be needed to examine whether the effects of direct hemispheric presentation are always greater for negative information than for positive or neutral information or whether the benefit for negative information can be modulated on the basis of stimulus characteristics (e.g., the arousal level of the stimulus, whether the stimulus is a word or an object) or task demands (e.g., how attention is directed to the information).

In summary, the results of the present study indicate that when information is initially processed directly in the LVF/RH, there is a lasting benefit in memory for the visual details of negative objects. Thus, the RH specialization for processing both negative affect (e.g., Natale et al., 1983) and exemplar-specific details (e.g., Marsolek, 1999) has critical implications for the type of information that is encoded into episodic long-term memory. By contrast, when information is presented directly to the RVF/LH, there is an increased tendency to remember only the gist of the information, and this tendency is not influenced by the emotional valence of the information. These results emphasize the complex interplay between emotional valence, hemispheric processing, and memory specificity and highlight the importance of considering differences in how the two hemispheres process information when examining the effects of emotional valence on memory.

References

- Berrini, R., Della Sala, S., Spinnler, H., Sterzi, R., & Vallar, G. (1982). In eliciting hemisphere asymmetries which is more important: The stimulus input side or the recognition side? A tachistoscopic study on normals. *Neuropsychologia*, *20*, 91–94.
- Borod, J. C. (1992). Interhemispheric and intrahemispheric control of emotion: A focus on unilateral brain damage. *Journal of Consulting and Clinical Psychology*, *60*, 339–348.
- Bourne, V. J. (2008). Chimeric faces, visual field bias, and reaction time bias: Have we been missing a trick? *Laterality*, *13*, 92–103.
- Burgund, E. D., & Marsolek, C. J. (2000). Viewpoint-invariant and viewpoint-dependent object recognition in dissociable neural subsystems. *Psychonomic Bulletin & Review*, *7*, 480–489.
- Collins, M. A., & Cooke, A. (2005). A transfer appropriate processing approach to investigating implicit memory for emotional words in the cerebral hemispheres. *Neuropsychologia*, *43*, 1529–1545.
- Coltheart, M. (1981). The MRC psycholinguistic database. *The Quarterly Journal of Experimental Psychology*, *33A*, 497–505.
- Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, *20*, 125–151.
- Davidson, R. J. (1995). Cerebral asymmetry, emotion, and affective style. In R. J. Davidson, & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 361–387). Cambridge, MA: MIT Press.
- Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, *3*, 11–20.
- Evans, K. M., & Federmeier, K. D. (2007). The memory that's right and the memory that's left: Event-related potentials reveal hemispheric asymmetries in the encoding and retention of verbal information. *Neuropsychologia*, *45*, 1777–1790.
- Federmeier, K. D., & Benjamin, A. S. (2005). Hemispheric asymmetries in the time course of recognition memory. *Psychonomic Bulletin & Review*, *12*, 993–998.
- Garoff, R. J., Slotnick, S. D., & Schacter, D. L. (2005). The neural origins of specific and general memory: The role of the fusiform cortex. *Neuropsychologia*, *43*, 847–859.
- Grünh, D., Scheibe, S., & Baltes, P. B. (2007). Reduced negativity effect in older adults' memory for emotional pictures: The heterogeneity-homogeneity list paradigm. *Psychology and Aging*, *22*, 644–649.
- Hannay, H. J., & Malone, D. R. (1976). Visual field effects and short-term memory for verbal material. *Neuropsychologia*, *14*, 203–209.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2006). Memory for specific visual details can be enhanced by negative arousing content. *Journal of Memory and Language*, *54*, 99–112.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007a). Effects of emotion on memory specificity: Memory trade-offs elicited by negative

- visually arousing stimuli. *Journal of Memory and Language*, *56*, 575–591.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007b). Effects of emotion on memory specificity in young and older adults. *Journals of Gerontology: Series B: Psychological Sciences and Social Sciences*, *62B*, P208–P215.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007c). How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience*, *19*, 1872–1887.
- Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemispheres: A computational approach. *Psychological Review*, *94*, 148–175.
- Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 723–735.
- Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, *39*, 184–199.
- Kucharska-Pietura, K. (2006). Disordered emotional processing in schizophrenia and one-sided brain damage. *Progress in Brain Research*, *156*, 467–479.
- Landis, T. (2006). Emotional words: What's so different from just words? *Cortex*, *42*, 823–830.
- Lee, G. P., Loring, D. W., Meader, K. J., & Brooks, B. B. (1990). Hemispheric specialization for emotional expression: A reexamination of results from intracarotid administration of sodium amobarbital. *Brain and Cognition*, *12*, 267–280.
- Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 375–386.
- Marsolek, C. J. (1999). Dissociable neural subsystems underlie abstract and specific object recognition. *Psychological Science*, *10*, 111–118.
- Marsolek, C. J., & Burgund, E. D. (2008). Dissociable neural subsystems underlie visual working memory for abstract categories and specific exemplars. *Cognitive, Affective, & Behavioral Neuroscience*, *8*, 17–24.
- Marsolek, C. J., Schacter, D. L., & Nichols, C. D. (1996). Form-specific visual priming for new associations in the right cerebral hemisphere. *Memory & Cognition*, *24*, 539–556.
- Marsolek, C. J., Squire, L. R., Kosslyn, S. M., & Lulenski, M. E. (1994). Form-specific explicit and implicit memory in the right cerebral hemisphere. *Neuropsychology*, *8*, 588–597.
- Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996, October 31). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*, 812–815.
- Natale, M., Gur, R. E., & Gur, R. C. (1983). Hemispheric asymmetries in processing emotional expressions. *Neuropsychologia*, *21*, 555–565.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.
- Paradiso, S., Johnson, D. L., Andreasen, N. C., O'Leary, D. S., Watkins, G. L., Ponto, L. L., & Hichwa, R. D. (1999). Cerebral blood flow changes associated with attribution of emotional valence to pleasant, unpleasant, and neutral visual stimuli in a PET study of normal subjects. *American Journal of Psychiatry*, *156*, 1618–1629.
- Payne, J. D., Stickgold, R., Swanberg, K., & Kensinger, E. A. (in press). Sleep preferentially enhances memory for emotional components of scenes. *Psychological Science*.
- Sackeim, H. A., Greenberg, M. S., Weiman, A. L., Gur, R. C., Hungerbuehler, J. P., & Geschwind, N. (1982). Hemispheric asymmetry in the expression of positive and negative emotions: Neurological evidence. *Archives of Neurology*, *39*, 210–218.
- Sato, W., & Aoki, S. (2006). Right hemispheric dominance in processing of unconscious negative emotion. *Brain and Cognition*, *62*, 261–266.
- Schaffer, C. E., Davidson, R. J., & Saron, C. (1983). Frontal and parietal electroencephalogram asymmetry in depressed and nondepressed subjects. *Biological Psychiatry*, *18*, 753–762.
- Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D., & Schacter, D. L. (2003). Neural mechanisms of visual object priming: Evidence for perceptual and semantic distinctions in fusiform cortex. *Neuroimage*, *19*, 613–626.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology: General*, *117*, 34–50.
- Starkstein, S. E., Robinson, R. G., Honig, M. A., Parikh, R. M., Joselyn, J., & Price, T. R. (1989). Mood changes after right-hemisphere lesions. *British Journal of Psychiatry*, *155*, 79–85.
- Strange, B. A., Henson, R. N., Friston, K. J., & Dolan, R. J. (2000). Brain mechanisms for detecting perceptual, semantic, and emotional deviance. *Neuroimage*, *12*, 425–433.

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