Behavioral/Cognitive

A Single-System Model Predicts Recognition Memory and Repetition Priming in Amnesia

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We challenge the claim that there are distinct neural systems for explicit and implicit memory by demonstrating that a formal single-system model predicts the pattern of recognition memory (explicit) and repetition priming (implicit) in amnesia. In the current investigation, human participants with amnesia categorized pictures of objects at study and then, at test, identified fragmented versions of studied (old) and nonstudied (new) objects (providing a measure of priming), and made a recognition memory judgment (old vs new) for each object. Numerous results in the amnesic patients were predicted in advance by the single-system model, as follows: (1) deficits in recognition memory and priming were evident relative to a control group; (2) items judged as old were identified at greater levels of fragmentation than items judged new, regardless of whether the items were actually old or new; and (3) the magnitude of the priming effect (the identification advantage for old vs new items) overall was greater than that of items judged new. Model evidence measures also favored the single-system model over two formal multiple-systems models. The findings support the single-system model, which explains the pattern of recognition and priming in amnesia primarily as a reduction in the strength of a single dimension of memory strength, rather than a selective explicit memory system deficit.

Key words: amnesia; computational model; long-term memory; memory systems; recognition memory; repetition priming

Introduction

One of the most influential distinctions in the cognitive neuroscience of memory is between explicit and implicit long-term memory. Explicit memory refers to conscious recollection of prior experiences. Implicit memory refers to changes in behavior that are due to prior experience, but are unaccompanied by conscious recollection of those experiences (Schacter, 1987). Implicit memory is commonly shown via repetition priming, which is a change or facilitation in identification, production, or detection of an item (e.g., a picture of an object) as a result of prior exposure to the same or a similar item. Strikingly, despite profound deficits in explicit memory tasks such as recognition—in which participants judge whether items have been presented before in a certain context—individuals with amnesia can show normal levels of repetition priming (Hamann and Squire, 1997). This dissociation is widely regarded as some of the strongest evidence for the proposal that functionally and neurally distinct explicit and implicit memory systems exist in the brain: recognition is driven by

an explicit (declarative/conscious) memory system located in the medial temporal lobes (damaged in amnesia), whereas priming is driven by implicit (nondeclarative/unconscious) memory systems in modality-specific neocortical regions (Tulving and Schacter, 1990; Gabrieli, 1998; Squire, 2009). Of primary interest here is the proposal that recognition and priming are driven by distinct explicit and implicit memory sources (Squire, 2009).

An alternative perspective is that recognition and repetition priming are driven by the same memory system or source. This view has been formalized in a single-system (SS) model of recognition and priming (Berry et al., 2006, 2008a,b, 2010, 2012; Shanks and Berry, 2012). Surprisingly, this model can explain numerous results in healthy adults that on the surface appear to be indicative of multiple systems; it even predicts results that are not predicted by multiple-systems versions of the model and can provide better fits to the data (Berry et al., 2012).

Here we provide a critical test of the SS model by applying it to data from amnesia. We also compare its fit to two formal multiple-systems models. We test a relatively homogeneous and well characterized group of amnesic patients that is atypically large (n = 24; Hayes et al., 2012). The patients had Korsakoff's syndrome (KS), a chronic disorder that is often caused by severe alcoholism and thiamine deficiency that results in diencephalic, frontal, and hippocampal brain damage (Le Berre et al., 2014). It is characterized by anterograde and retrograde amnesia (Kopelman et al., 2009; Fama et al., 2012; Kessels and Kopelman, 2012; Race and Verfaellie, 2012). Findings from patients with KS have

played a central role in the formulation of multiple-systems views (Hayes et al., 2012), and implicit memory is widely regarded to be preserved in KS (Kopelman et al., 2009; Oudman et al., 2011). In the current investigation, participants categorized pictures of familiar objects (e.g., an elephant) at study. In the test phase, participants identified fragmented versions of old (studied) and new objects (providing a measure of priming), and made a recognition memory judgment (old/new) after identifying each object.

Materials and Methods

Participants. Twenty-four patients (16 male; mean age, 50.2 years; SD, 7.7 years) with Korsakoff's amnesia were recruited via the Korsakoff Clinic of the Vincent van Gogh Institute for Psychiatry, Venray, The Netherlands (KOR group). All patients fulfilled the criteria for alcohol-induced persisting amnestic disorder (American Psychiatric Association, 2000) and Korsakoff's syndrome (Kopelman, 2002). The diagnoses were supported by the patients' medical history and neuropsychological assessment, and all participants had anterograde amnesia, performing in the impaired range on the Rivermead Behavioral Memory Test [RBMT; Wilson et al., 1989; Van Balen et al., 1996; total profile score: mean score, 6.7; SD, 4.0 (scoring: 17–21, poor memory; 10–16, mildly impaired; 0–9, severely impaired)], as well as retrograde amnesia for their biographical history. Premorbid intelligence was estimated using the Dutch version of the National Adult Reading Test (NART; Schmand et al., 1991), with IQs in the below-average to average range, which was in agreement with the patients' educational levels (mean NART-IQ score, 93.8; SD, 12.5; mean educational level, 3.9; SD, 1.1), where education level was assessed in seven categories based on the Dutch educational system, as follows: 1, primary school; 7, academic degree (Verhage, 1964). Neuroradiological findings (CT or MRI) showed abnormalities associated with KS, such as (diencephalic) atrophy or white-matter lesions (Pitel et al., 2012). No brain abnormalities were found that countered the clinical diagnosis (e.g., large strokes, tumors). All patients were abstinent from alcohol since their admittance to the clinic (>3 months before testing), none was in the acute Wernicke phase of the syndrome, and none fulfilled the criteria for alcohol-related dementia (Oslin et al., 1998).

The control (CON) group also consisted of 24 individuals, matched in terms of age (mean age, 50.2 years; SD, 13.6 years; $t_{(46)} = 0.59$, $p = 0.56$), premorbid IQ (mean NART-IQ score, 96.4; SD, 12.6; $t_{(46)} = 0.72$, $p = 0.47$), and the proportion of males and females. Exclusion criteria for the control subjects were a self-reported history of neurologic or psychiatric disorder, or subjective cognitive complaints. Level of education (mean level, 5.3; SD, 0.8) was significantly higher in the CON group than the KOR group (Mann–Whitney $U = 90.50$, $p < 0.01$); however, this variable was not found to be significantly correlated with subsequent measures of recognition or priming performance at test within each group (r values ranged from −0.14 to 0.23).

Materials. The stimuli were 80 color photographs of familiar objects (e.g., a bicycle, a guitar). All stimuli were presented on a computer monitor against a white background. Each object subtended ∼7.5° of visual angle in the horizontal and vertical. Stimuli were arranged into two 40-item lists. Each list acted as the studied or new stimuli equally often across participants. Approximately half of the objects in each list were larger than a shoebox. All instructions were presented in Dutch.

Procedure. During the study phase, participants were told that they would be presented with pictures of objects and that they must decide whether each object was smaller or larger in size than a shoebox, indicating their response with a button press. The sequence of events on each trial was as follows: (1) a central fixation point ("+") was presented for 2000 ms; (2) the object was then presented for 2000 ms; and (3) if a response had been made, the next trial then commenced, and if a response had not been made, a blank screen was presented until a response was made. For the duration of the study phase, the reminder cue "Is the object smaller or larger than a shoebox? Z = smaller, M = larger" remained visible toward the bottom of the screen. The order of presentation of items was randomly determined for each participant. There was a short (maximum time, 5 min) retention interval before the test phase
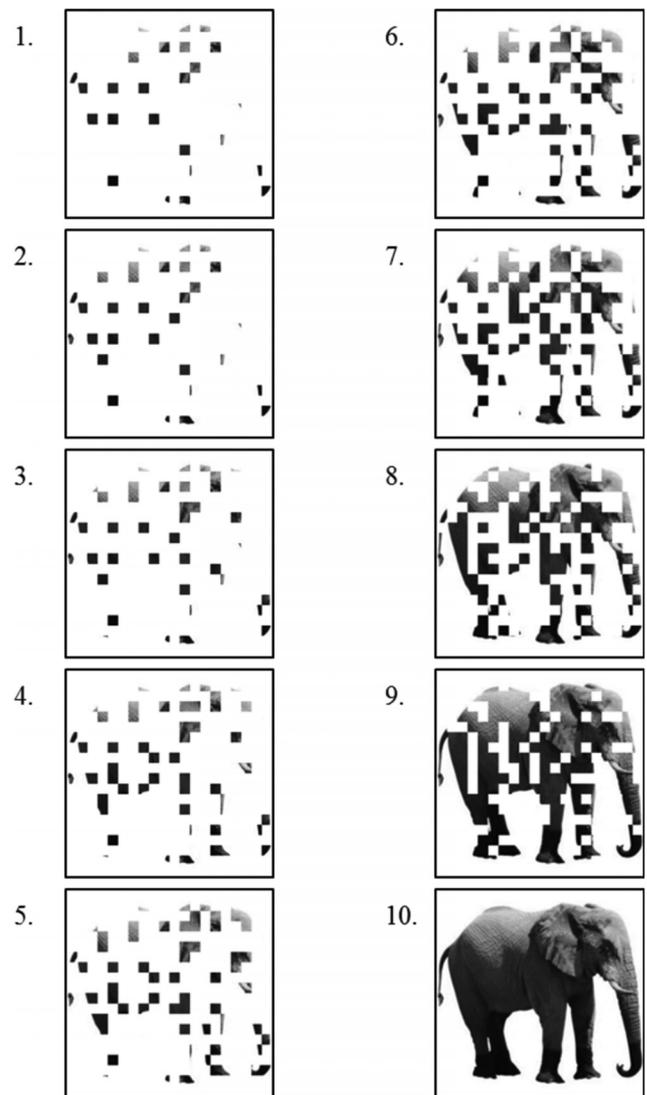
Figure 1. Example of a fragmented stimulus used in the identification portion of a CID-R trial at test. An object was initially presented at a highly fragmented level (level 1). Participants were instructed to try to identify the item at the most fragmented level they could. If the item could not be identified, a button press revealed a less fragmented version of the object (up to level 10).

commenced, during which standardized tests (e.g., NART) were administered.

A continuous identification with recognition (CID-R; Stark and McClelland, 2000) procedure was used to present each item at test. On each trial, an item was initially presented in an extremely fragmented form. The instructions for the test phase informed participants that the object would initially be difficult to identify, but that each press of the spacebar would reveal a less fragmented version of the object (up to 10 levels; Fig. 1). Their task was to identify each object at the most fragmented level possible. Participants were told not to try to identify the object until they were sure that they could do so. Identification accuracy was near the ceiling in both groups, although it was higher in the CON group [proportion of trials correct: CON group: mean, 0.998; KOR group: mean, 0.958 (excluding one outlier in the KOR group who only identified 0.49 proportion of trials correctly; the recognition/priming results reported later are not affected if this participant is excluded)]. Trials on which an incorrect identification occurred were not excluded from the analysis to preserve recognition data; however, the qualitative pattern of results did not differ when they were excluded (one exception to this was that Prediction 3 in the KOR group was only significant on a one-tailed test). The prompt "Press SPACE to reveal more of the drawing, and press ENTER at the earliest point that you can identify the item

correctly" remained on screen during the clarification procedure. When participants pressed enter, a black outlined box and prompt ("Type your response and then press ENTER") appeared beneath the fragmented object. After a response was typed, the nonfragmented version of the object was then presented with the prompt, "Was the object presented in the first stage? 1 = sure no, 2 = probably no, 3 = probably yes, 4 = sure yes." After participants made their recognition response, a blank screen was presented for 2000 ms before the next test trial was presented. There were 80 trials in total (40 old and 40 new). To evenly distribute old and new trial types across the test phase, trials were randomly arranged into four blocks with an equal number of old and new trials in each block (there was no indication of block transition to participants).

To create fragmented versions of each image, each 400×400 pixel image was divided into 400 20×20 pixel squares. At each of 10 possible fragmentation levels, a fixed proportion of the squares containing the target image was displayed. The proportion of squares displayed at each fragmentation level, x, was calculated as $0.75^{(10-x)}$, $x \in [1, 10]$. Thus, the fragmentation procedure was such that the rate of clarification was relatively slow across the initial fragmentation levels and more rapid in the later stages. This was done to increase the difficulty of the task in the early stages of the procedure.

Recognition responses were collapsed across confidence ratings 1 and 2 for "new" judgments, and ratings 3 and 4 for "old" judgments. This was done because a large proportion of participants made no responses in at least one of the confidence $[(1-4) \times$ item status (old, new)] response categories (79% of individuals in the KOR group, and 71% of individuals in the CON group). Recognition performance was measured with P_r, which was calculated as $H - F$, where $H = p(\text{hit})$, and $F = p(\text{false alarm})$; d' was also calculated as $z(H) - z(F)$, where a "hit" is an old judgment to an old item, and a "false alarm" is an old judgment to a new item. Response bias was measured with C ($C = -0.5[z(H) + z(F)]$). For the calculation of d' and C, a correction was applied when calculating H and F for each individual [i.e., $H = $ (no. of hits $+ 0.5$)/(no. of possible hits $+ 1$), and $F = $ (no. of false alarms $+ 0.5$)/(no. of possible false alarms); Snodgrass and Corwin, 1988]. This enabled the calculation of d' and C for participants for whom H or F was equal to 1 or 0. An α level of 0.05 was used for all statistical tests, and all t tests were two tailed, unless indicated otherwise. Effect sizes are indicated by Cohen's d (for t tests) and η_p^2 (for ANOVA).

Reliability of the recognition and priming measures. Prior research has shown that it is important to take into account the reliability of the tasks used to measure recognition and priming when comparing performance (Buchner and Wippich, 2000). Accordingly, the reliability of the recognition and priming measures was calculated using split-half correlations. Each participant's dataset was split into odd and even trials, and then P_r and priming measures were calculated for the trials in each of these halves. The split-half correlation for recognition/priming is the Pearson correlation of the recognition/priming measures for each half, across participants. Importantly, both recognition and priming were highly reliable (recognition: $r_{(46)} = 0.91$, $p < 0.001$; priming: $r_{(46)} = 0.56$, $p < 0.001$). The greater reliability of the recognition task is consistent with previous research (Buchner and Wippich, 2000); however, when each group was analyzed individually, the reliability of recognition was greater than that of priming only in the KOR group, and not the CON group (where the reliability of recognition and priming was approximately equal; KOR group: recognition, $r_{(22)} = 0.84$, $p < 0.001$; priming, $r_{(22)} = 0.47$, $p = 0.02$; CON group: recognition, $r_{(22)} = 0.50$, $p = 0.013$; priming, $r_{(22)} = 0.58$, $p = 0.003$).

Formal single-system and multiple-systems models. Full details of the models are given in the study by Berry et al. (2012). The SS model is based on signal detection theory (Green and Swets, 1966) and assumes that during the test phase each item is associated with a memory strength value, f, which is a normally distributed, random variable with mean (μ) and SD σ_f [i.e., $f \sim N(\mu, \sigma_f)$]. The mean f of old items can be greater than of new items because of prior study (i.e., $\mu_{\text{old}} \geq \mu_{\text{new}}$). The value of f for an item is used to derive its recognition judgment *and* its measure of priming. To generate a recognition judgment, random, normally distributed noise, e_r, is first added to f to produce the judgment measure J_r [i.e., $J_r = f + e_r$, where $e_r \sim N(0, \sigma_r)$]. If J_r exceeds a particular threshold of

strength, C, the item will be judged old, otherwise it will be judged new. For the priming task, greater values of f will tend to result in better performance in the task. For example, if the task is to identify fragmented versions of an object (fragment identification), the greater the value of f for an item, the greater the level of fragmentation at which it will be identified. Importantly, however, f is combined with another independent source of random normally distributed noise, e_p, to derive the priming measure [i.e., $\text{ID} = b - sf + e_p$, where ID is the level of fragmentation at which identification occurs; b and s are scaling parameters; b is the ID intercept; s is the rate of change in ID with f; and $e_p \sim N(0, \sigma_p)$]. Both of the task-specific noise variables e_r and e_p have mean values equal to zero.

The SS model can be modified to create two "multiple-systems" versions of the model—the MS1 and MS2 models. The MS1 model is the same as the SS model except that one "explicit" memory strength signal, f_r, drives recognition [where $f_r \sim N(\mu_r, \sigma_f)$], whereas a separate "implicit" memory signal, f_p, drives priming [where $f_p \sim N(\mu_p, \sigma_f)$]. As in the SS model, f_r and f_p are combined with task-specific sources of noise (e_r and e_p) to produce the recognition judgment (i.e., $J_r = f_r + e_r$) and priming measure (i.e., $\text{ID} = b - sf_p + e_p$). Importantly, however, f_r and f_p are uncorrelated [i.e., $r(f_r, f_p) = 0$], and the mean explicit strength of old items ($\mu_{\text{r|old}}$) can vary independently of the mean implicit strength of old items ($\mu_{\text{r|old}}$) across individuals/conditions. This allows the model to produce dissociations at the level of individual items (e.g., stochastic independence; Tulving et al., 1982; Poldrack, 1996) and also at the level of group/condition (e.g., independent effects of a variable upon recognition and priming, such as the dissociation in amnesia). Thus, this model represents a relatively strong interpretation of the idea that explicit and implicit memory systems are independent (Tulving et al., 1982).

Another model, the MS2 model, represents a weaker interpretation of the idea that there is independence between systems (Berry et al., 2012). This model is identical to the MS1 model except that the explicit and implicit strengths of individual items may be positively correlated (with correlation w). A correlation could arise, for example, via distinctiveness: a more distinctive item may be better encoded into both the explicit and implicit memory systems. This gives the MS2 model greater flexibility, allowing it to reproduce associations between recognition and priming measures at the level of individual items (like the SS model). In fact, the MS2 model subsumes the SS and MS1 models as special cases of it, and the MS2 model can therefore, in principle, produce any result that the SS and MS1 models can achieve (Berry et al., 2012). When the correlation between f_r and f_p is 1 [i.e., $r(f_r, f_p) = 1$], and the mean f_r and f_p values of old items are equal (i.e., $\mu_{\text{r|old}} = \mu_{\text{p|old}}$), $f_r = f_p$, and so the model reduces to the SS model; when the correlation between f_r and f_p is zero [i.e., $r(f_r, f_p) = 0$], the model reduces to the MS1 model (Berry et al., 2012).

Model fitting. Models were fit using maximum likelihood estimation (full details are given in Berry et al., 2012). The likelihood of each identification level (ID) and judgment (Z) combination is given by the following function:

$$L(Z, \text{ID}|X) = [\Phi(C_j|\mu_{J_r|\text{ID},X}, \sigma_{J_r|\text{ID}}^2) - \Phi(C_{j-1}|\mu_{J_r|\text{ID},X}, \sigma_{J_r|\text{ID}}^2)] \times$$

$$\phi(\text{ID}|b - s\mu_{p|X}, \sigma_{\text{ID}}^2),$$

where $X = $ old, new; Φ is the cumulative normal distribution function; ϕ is the normal density function; $\sigma_{\text{ID}}^2 = s^2\sigma_f^2 + \sigma_p^2$; $\mu_{J_r|\text{ID},X}$; and $\sigma_{J_r|\text{ID}}^2$ are the mean and variance of the conditional distribution of J_r given ID, $j = 1$ when $Z = $ "new" (N), and $j = 2$ when $Z = $ "old" (O); $C_0 = -\infty$, $C_1 = C$ and $C_2 = \infty$. $\mu_{J_r|\text{ID},X}$ and $\sigma_{J_r|\text{ID}}^2$ are calculated as follows:

$$\mu_{J_r|\text{ID},X} = \mu_{r|X} - \frac{ws\sigma_f^2(\text{ID} - b + s\mu_{p|X})}{s^2\sigma_f^2 + \sigma_p^2},$$

and

$$\sigma_{J_r|\text{ID}}^2 = \sigma_f^2 + \sigma_r^2 - \frac{w^2s^2\sigma_f^4}{s^2\sigma_f^2 + \sigma_p^2},$$

where $\mu_{r|\text{new}} = 0$ when $X = $ new, and $\mu_{r|\text{old}} \geq 0$ when $X = $ old; $\mu_{p|\text{new}} = 0$ when $X = $ new, and $\mu_{p|\text{old}} \geq 0$ when $X = $ old. In the SS model, $\mu_{r|\text{old}} = $

Table 1. Mean (SD) of the model parameters

Parameter	Meaning	Aggregate fits						Individual fits					
		SS		MS1		MS2		SS		MS1		MS2	
		KOR	CON	KOR	CON	KOR	CON	KOR	CON	KOR	CON	KOR	CON
$\mu_{r|old}$	$M(f_{r|old})$	0.69	2.48	0.72	2.49	0.72	2.49	1.06 (0.76)	2.66 (0.57)	1.01 (0.83)	2.66 (0.57)	1.01 (0.83)	2.66 (0.57)
$\mu_{p|old}$	$M(f_{p|old})$	$=\mu_{r|old}$	$=\mu_{r|old}$	0.51	2.18	0.51	2.18	$=\mu_{r|old}$	$=\mu_{r|old}$	0.83 (0.66)	2.54 (1.20)	0.92 (0.69)	2.53 (1.15)
w	$r(f_r, f_p)$	$=1$	$=1$	$=0$	$=0$	1.00	1.00	$=1$	$=1$	$=0$	$=0$	0.82 (0.35)	0.62 (0.43)
C	Judgment criterion	0.69	1.45	0.71	1.45	0.71	1.46	0.80 (0.83)	1.55 (0.43)	0.77 (0.78)	1.55 (0.43)	0.77 (0.78)	1.55 (0.43)
b	ID intercept	6.51	6.23	6.45	6.18	6.45	6.18	6.53 (0.90)	6.22 (1.47)	6.53 (0.89)	6.22 (1.47)	6.53 (0.89)	6.22 (1.47)
s	ID slope	0.68	0.31	$=$ SS	$=$ SS	$=$ SS	$=$ SS	0.57 (0.55)	0.25 (0.21)	$=$ SS	$=$ SS	$=$ SS	$=$ SS
σ_p	$SD(e_p)$	1.88	2.36	1.89	2.36	1.88	2.36	1.59 (0.32)	1.73 (0.38)	1.59 (0.32)	1.73 (0.38)	1.58 (0.32)	1.72 (0.38)
σ_f	$SD(f_r), SD(f_p)$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$	$=1/\sqrt{2}$
σ_r	$SD(e_r)$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$	$=\sigma_f$
$M(e_p)$	M priming task noise	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$
$M(e_r)$	M recognition task noise	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$
$\mu_{r|new}$	$M(f_{r|new})$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$	$=0$
$\mu_{p|new}$	$M(f_{p|new})$	$=\mu_{r|new}$	$=\mu_{r|new}$	$=0$	$=0$	$=0$	$=0$	$=\mu_{r|new}$	$=\mu_{r|new}$	$=0$	$=0$	$=0$	$=0$

A value preceded by an equals sign indicates that the value was fixed, otherwise it was free to vary in fitting the data.

$\mu_{p|old} = \mu_{old}$, and $w = 1$. In the MS1 model, $w = 0$; in the MS2 model, $0 \leq w \leq 1$.

In fitting the models to the data, an automated procedure was used to find the parameter values that maximize the summed log likelihood across trials. A full list of parameters (both free and fixed) is given in Table 1. The values of certain parameters are nonidentifiable and were therefore fixed such that they act as scaling parameters (Berry et al., 2012), as follows: SS model, $\mu_{new} = 0$; MS1/MS2 models, $\mu_{r|new} = \mu_{p|new} = 0$; $M(e_p) = M(e_r) = 0$; $\sigma_f = \sigma_r = \sqrt{0.5}$; finally, the value of s in the MS1 and MS2 models was fixed to that of the SS model. Fixing σ_f and σ_r to $\sqrt{0.5}$ means that the SD of J_r is equal to 1 (because $\sigma_{Jr} = \sqrt{(\sigma_f^2 + \sigma_r^2)}$), and $\mu_{r|old}$ can therefore be interpreted as d'. We have previously shown that whether s is fixed or free to vary in the MS1 and MS2 models does not affect their fit (Berry et al., 2012).

This leaves the following five free parameters in the SS model: μ_{old}, the mean strength of the old item distribution; C, the old judgment criterion; b, the ID intercept; s the rate of change in the ID level with changes in f; and σ_p, the variance of e_p, the noise associated with the priming task. The MS1 model also has the following five free parameters: $\mu_{r|old}$, the mean explicit memory strength of the old item distribution; $\mu_{p|old}$, the mean implicit memory strength of the old item distribution; C, the old judgment criterion; b, the ID intercept; and σ_p, the variance of e_p. The MS2 model has the following six free parameters: $\mu_{r|old}$, the mean explicit memory strength of the old item distribution; $\mu_{p|old}$, the mean implicit memory strength of the old item distribution; C, the old judgment criterion; b, the ID intercept; σ_p, the variance of e_p; and w, the correlation between f_r and f_p.

It is usually preferable to fit the models to each participant's data; however, this was not possible for all participants because the model parameters could not be estimated for participants who did not make at least one hit, miss, false alarm, or correct rejection response. Accordingly, the models were fit to (1) the data aggregated across the 24 participants within each group and (2) to each individual's data, providing that the individual made at least one hit, miss, false alarm, and correct rejection response (CON group, $n = 19$; KOR group, $n = 15$). We report the Akaike information criterion (AIC, Akaike, 1973) and the Bayesian information criterion (BIC, Schwarz, 1978) measures of fit because both are frequently reported in model comparisons. We place more emphasis on the AIC because our previous investigations indicated that the true generative model can be more reliably identified with this measure (Berry et al., 2012).

Given the best-fitting parameter values for a model, the expected model results can be calculated analytically as follows: $P(\text{hit}) = 1 - \Phi(C - \mu_{r|old})$; $P(\text{false alarm}) = 1 - \Phi(C)$; $d' = \mu_{r|old}$; $E[\text{ID}|\text{new}] = b$; $E[\text{ID}|\text{old}] = b - s\mu_{p|old}$; priming effect $= s\mu_{p|old}$.

The expected values of ID conditional on judgment Z are given by the following function:

$$E(\text{ID}|Z,X) = b - s\mu_{p|X} + \frac{sw\sigma_f^2}{\sigma_{Jr}} \frac{\phi\left(\frac{C_j - \mu_{r|X}}{\sigma_{Jr}}\right) - \phi\left(\frac{C_{j-1} - \mu_{r|X}}{\sigma_{Jr}}\right)}{\Phi\left(\frac{C_j - \mu_{r|X}}{\sigma_{Jr}}\right) - \Phi\left(\frac{C_{j-1} - \mu_{r|X}}{\sigma_{Jr}}\right)},$$

where $\sigma_{Jr} = \sqrt{(\sigma_f^2 + \sigma_r^2)}$; $j = 1$ when $Z = N$; and $j = 2$ when $Z = O$; $C_0 = -\infty$; $C_1 = C$; and $C_2 = \infty$. Thus, the equation gives the expected ID of hits ($E[\text{ID}|H]$) when $X = $ old and $Z = O$; it gives the expected ID of false alarms ($E[\text{ID}|F]$) when $X = $ new and $Z = O$. Similarly, the equation gives the expected ID of misses ($E[\text{ID}|M]$) when $X = $ old and $Z = N$; and it gives the expected ID of correct rejections ($E[\text{ID}|CR]$) when $X = $ new and $Z = N$.

In the data, because the mean ID for items judged old/new are weighted means, the expected ID for items judged old/new are given by the weighted expected IDs to hits and false alarms (items judged old), or misses and correct rejections (items judged old), hence:

$$E[\text{ID}|Z = O] = \frac{P(\text{H})E[\text{ID}|\text{H}] + P(\text{F})E[\text{ID}|\text{F}]}{P(\text{H}) + P(\text{F})},$$

and

$$E[\text{ID}|Z = N] = \frac{[(1 - P(\text{H})E[\text{ID}|\text{M}] + [(1 - P(\text{F})]E[\text{ID}|\text{CR}])}{2 - P(\text{H}) - P(\text{F})},$$

The overall fluency effect (see below) can be calculated as $E[\text{ID}|Z = N] - E[\text{ID}|Z = O]$.

We should note that the ID response variable is discrete but is modeled here as continuous (because $f_p \sim N(\mu_p, \sigma_f)$ and $\text{ID} = b - sf_p + e_p$). To justify this way of modeling ID, parameter recovery simulations were performed. In these simulations, first, recognition judgment and ID data (for 10,000 old/new items) were simulated from a given model. The parameter values used for this were the mean estimated parameter values for the KOR group (given on the right-hand side of Table 1). The simu-
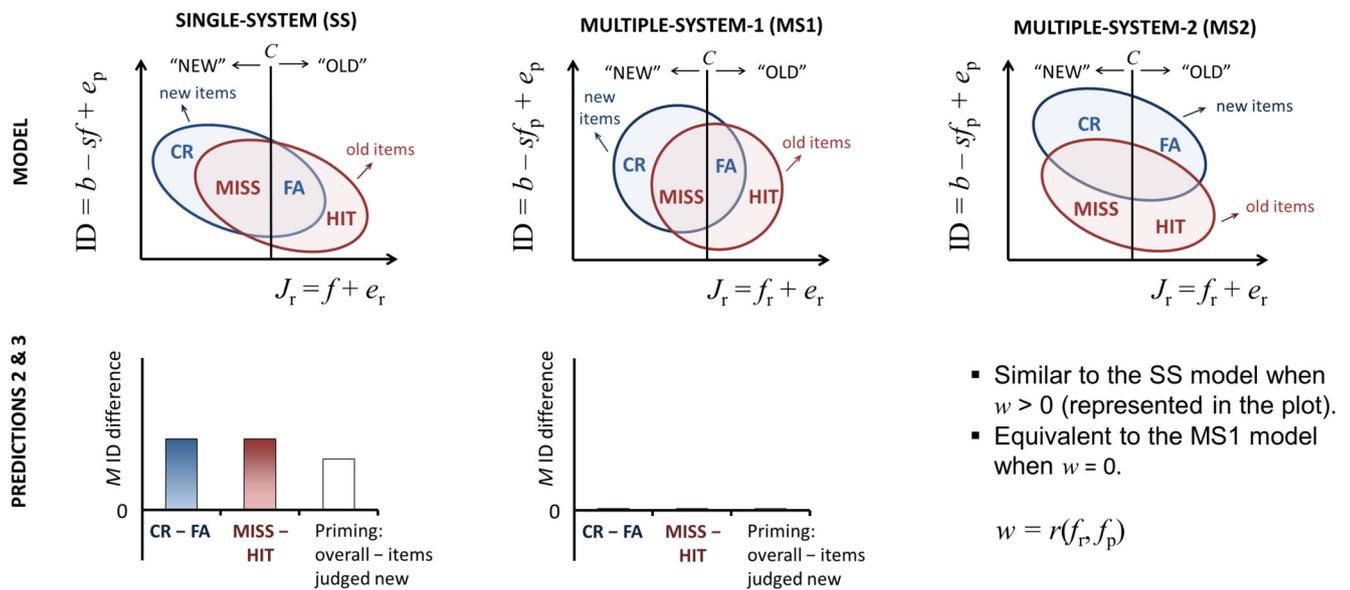
Figure 2. Model representations and Predictions 2 and 3. The top panels illustrate the relationship between the ID (identification level) and J_r variables in the models. The ellipses represent bivariate normal distributions of each class of item (old or new), cut horizontally and centered on a point that represents the mean J_r and ID for that class of item. Prediction 2 concerns whether ID levels are facilitated for items judged old within new and old items, that is, whether the mean ID of false alarms is less than that of correct rejections [CRs; i.e., CR − false alarm (FA)], and whether the mean ID of hits is less than of misses (i.e., MISS − HIT), where a correct rejection is a new judgment to a new item, a false alarm is an old judgment to a new item, a miss is a new judgment to an old item, and a hit is an old judgment to an old item. Prediction 3 concerns whether the priming effect overall (across all items) is greater than the priming effect for items judged new. Priming is calculated as mean ID(new items) − mean ID(old items); priming for items judged new is calculated as mean ID(CR) − mean ID(FA). The SS model predicts positive differences between ID(CR) − ID(MISS), ID(MISS) − ID(HIT), and priming − priming items judged new. The MS1 model predicts no differences. The MS2 model predicts positive differences when the explicit and implicit strengths of an item are positively correlated (i.e., $w > 0$), and predicts no differences when there is no correlation (i.e., $w = 0$).

lated ID values were then rounded to the nearest integer; if the value was <1 or >10, then it was rounded to 1 or 10, respectively, thereby producing discretized ID data. The simulated ID and judgment data were then fit by the models as described above, and the estimates of the free parameters were compared with the values of the parameters that were originally used to simulate the data (i.e., the true parameter values). For all models, the estimated parameter values matched the true parameter values. This demonstrates that the parameters of the models can still be recovered, even though the ID data are discrete.

Another issue concerns the function used to relate f_p to ID level. The amount of a test picture revealed across levels varies by an exponential function, whereas the equation relating ID level to f_p in the models is linear. It is possible that an alternative function relating ID to f_p would provide a more complete characterization of the ID data and improve the performance of all of the models. However, most important for current purposes is that ID is modeled as a monotonically decreasing function of f_p in all models. We chose to model the ID variable in this way for consistency with previous applications of the models, and for ease of model specification.

Model predictions. Three key predictions are made by the SS model. These predictions follow from the assumption that greater values of f tend to lead to a greater likelihood of an old judgment and also better performance in the priming task (i.e., greater values of J_r and lower values of ID; Fig. 2). Prediction 1 is that, given a deficit in recognition in amnesic individuals, a deficit in priming should also be evident. This is because changes in μ_{old} will tend to affect overall levels of both recognition and priming. However, the effect on priming can be smaller in magnitude than for recognition because of the greater variance of the noise associated with the priming task that is typically assumed (Berry et al., 2006). The MS1 and MS2 models can reproduce any pattern of recognition and priming, and so do not make this prediction in advance.

Predictions 2 and 3 concern performance in the priming task when broken down by recognition response (Fig. 2). Prediction 2 is that, within old and new items, items that are judged old are likely to be identified at greater levels of fragmentation than items judged new (this is often referred to as a "fluency effect"; Conroy et al., 2005): Items with values of J_r that exceed the criterion C are judged old and tend to have larger f values than items judged

new. Because the same f value drives identification, items judged old will tend to be identified at more fragmented levels. Prediction 3 concerns the priming effect for items judged new. This effect has been reported in numerous studies, and on the surface appears to indicate that recognition and priming have distinct memorial bases since priming occurs in the absence of overt recognition (Berry et al., 2008a). The SS model predicts that the magnitude of the priming effect (i.e., the identification advantage of all old items relative to new items) will be greater than the priming effect within the subset of items judged new (i.e., the identification advantage for old items judged new relative to new items judged new). This is because values of J_r tend to be greater for old items than new items, even within the subset of items judged new. However, the difference in J_r between all old and new items is greater than the difference in J_r between old and new items within the subset of items judged new (Fig. 2). Because differences in J_r tend to reflect differences in f, the priming effect across all items will tend to be greater than the priming effect within the subset of items judged new. (Though differences in J_r do not always reflect differences in f, as is the case, for example, with false-alarm and miss responses; Berry et al., 2008a.) Predictions 2 and 3 are not made by the MS1 model because ID and J_r are uncorrelated within item type (Fig. 2). The MS2 model can produce the same results as the SS model with regard to Predictions 2 and 3, but the greater flexibility of this model means that it does not make these predictions in advance.

Results

SS model prediction 1
Recognition memory was significantly lower in the KOR group ($n = 24$) than in the CON group ($n = 24$; Figs. 3a, 4a): P_r, $t_{(46)} = 9.31$, $p < 0.001$ (Cohen's $d = 2.69$); d', $t_{(46)} = 8.21$, $p < 0.001$ (KOR group, d', 1.00; SE, 0.17; CON group, d', 2.64; SE, 0.11), consistent with the memory disorder in these individuals. Recognition was reliably greater than chance (i.e., d' or $P_r > 0$) in both groups (t values >5.31, d values >1.08), and there was no significant difference in C between the groups ($t_{(46)} = 1.23$, $p = 0.23$, $d = 0.36$: mean C: KOR group, 0.50; SE, 0.21; CON group, 0.23; SE, 0.08).
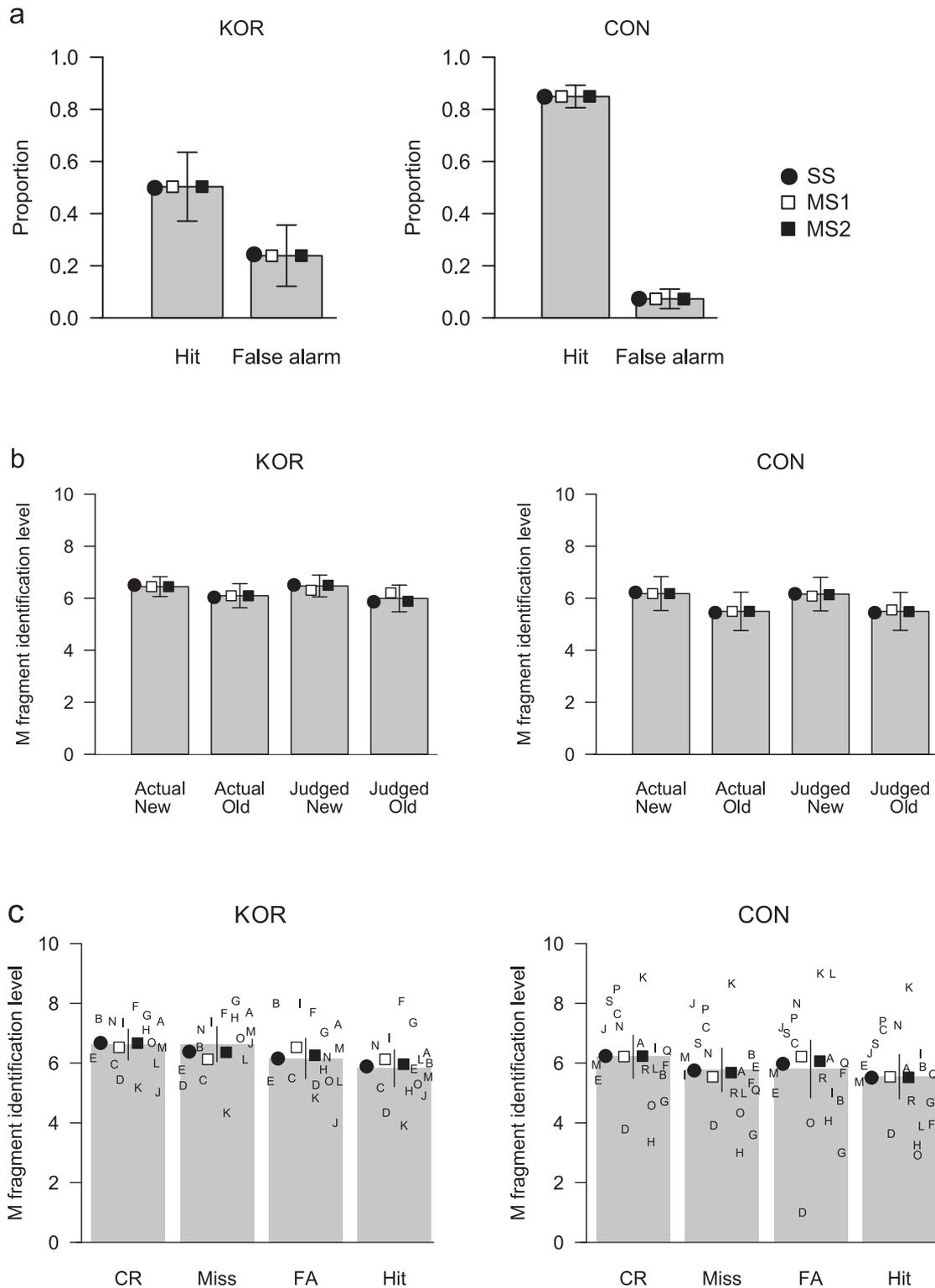
Figure 3. Recognition and priming task performance. ***a***, Proportion of hit and false-alarm responses in the KOR and CON groups. ***b***, Fragment identification performance according to whether the object during the test is actually new or old, or judged new or old. ***c***, Fragment identification performance classified according to the recognition response [correct rejection (CR), miss, false alarm (FA), hit] in the KOR and CON groups. Bars indicate experimental data (error bars indicate 95% confidence intervals of the mean). Symbols indicate the expected result from each model when fit to data aggregated across individuals (***a*** and ***b***; because the data in these figures are derived from all of the participants) or the mean expected result from each model when fit to each individual's data (***c***; because the data in these figures are derived from the subset of participants with responses in all four recognition categories). In ***c***, the letters represent the individuals in each group.

Priming was calculated as the mean identification level for new items minus the mean identification level for old items. Both groups showed reliable (i.e., >0) levels of priming: KOR group: mean, 0.35; SE, 0.11; $t_{(23)} = 3.18$, $p = 0.004$, $d = 0.65$; CON group: mean, 0.68; SE, 0.14; $t_{(23)} = 4.78$, $p < 0.001$, $d = 0.98$ (Figs. 3b, 4a). Crucially, priming was significantly lower in the KOR group than in the CON group ($t_{(46)} = 1.84$; $p = 0.036$, one-tailed; $d = 0.53$), as predicted by the SS model. Furthermore, there was
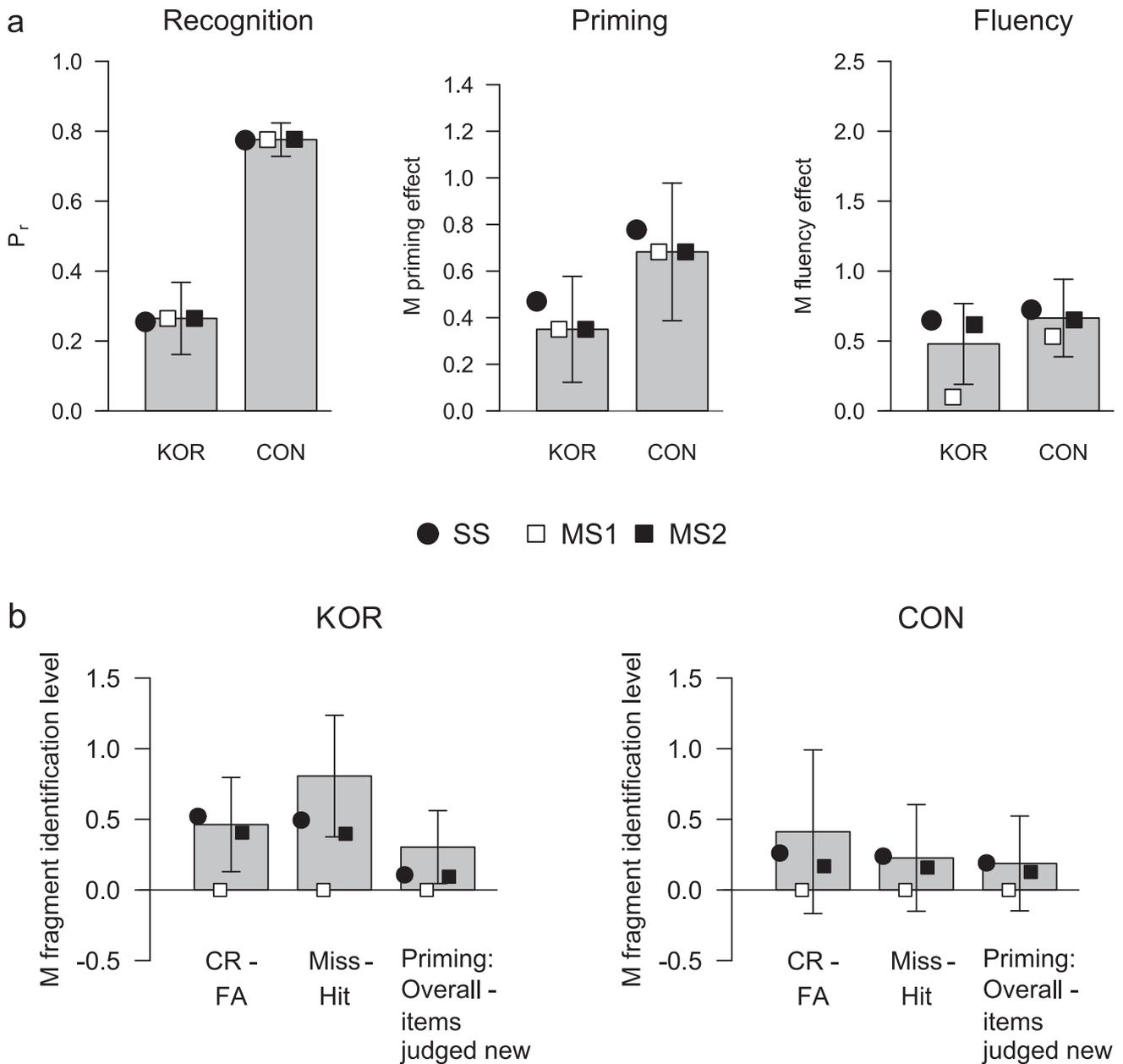
Figure 4. Model prediction results. ***a***, Recognition discrimination (P_r: proportion of hits − proportion of false alarms) and priming (i.e., fragment identification advantage for old objects) for the KOR and CON groups. Fluency effects (i.e., fragment identification advantage for objects judged old) across all items are also presented. Prediction 1 of the SS model is confirmed by lower recognition and priming in the KOR group than in the CON group. ***b***, Differences in the ID level for items judged old versus judged new within new and old item types, and differences in the priming effect (overall) and the priming effect of items judged new. Predictions 2 and 3 of the SS model are confirmed in the KOR group. Bars indicate experimental data (error bars indicate 95% confidence intervals of the mean). Symbols indicate the expected result from each model when fit to data aggregated across individuals (***a***; because the data are derived from all of the participants) or the mean expected result from each model when fit to each individual's data (***b***; because the data are derived from the subset of participants with responses in all four recognition categories).

no significant difference in the mean identification level for new items across groups (Fig. 3b; $t_{(46)} = 0.74$, $p = 0.47$, $d = 0.21$), which indicated that any difference in priming across groups could not be attributed to differences in baseline levels of performance in the task. Identifications were made at all possible fragmentation levels (range, 1–10 in both groups; interquartile range: KOR group, 5–8; CON group, 4–8).

SS model predictions 2 and 3
To test Predictions 2 and 3, the identification level of each item during testing was analyzed according to the following four pos-

sible recognition responses: a correct rejection is a new judgment to a new item; a false alarm is an old judgment to a new item; a miss is a new judgment to an old item; and a hit is an old judgment to an old item (Fig. 3c). A subset of participants made no responses in at least one of the four response categories, and so they were not included in the following analyses. There were five participants from the CON group: one had a hit rate of 1; and four had a false alarm rate of 0. Nine participants were also excluded from the KOR group on this basis: one had a hit rate of 1; one had a false alarm rate of 1; and seven had a false alarm rate of 0. The priming scores in the excluded participants were slightly

Table 2. Goodness-of-fit values for the models

Data fit	Group	SS				MS1				MS2			
		p	ln(L)	AIC*	BIC†	p	ln(L)	AIC*	BIC†	p	ln(L)	AIC*	BIC†
Aggregated	KOR (z = 1)	5	−5172.7	10,355.4	10,383.2	5	−5196.7	10,403.4	10,431.3	6	−5171.5	**10,355.1**	10,388.5
	CON (z = 1)	5	−5035.2	**10,080.4**	10,108.2	5	−5042.7	10,095.4	10,123.2	6	−5034.8	10,081.6	10,115.0
Individual	KOR (z = 15)	5	−2925.5	**6001.1**	6382.8	5	−2943.3	6036.7	6418.4	6	−2922.1	6024.2	6482.3
	CON (z = 19)	5	−3444.8	**7079.6**	7585.6	5	−3446.2	7082.4	7588.4	6	−3443.2	7114.5	7721.7

For the aggregate fits, data from all 24 participants are modeled as if from one participant (hence z = 1, where z is the (effective) number of participants modeled in each experiment). For the individual fits, it was not possible to model participants who had zero hit, miss, false alarm, or correct rejection responses (hence z values <24). A smaller AIC or BIC value indicates greater support for a model. BOLD indicates that the model fit the data best according to the AIC measure.

*The AIC is calculated as follows: $AIC = -2\ln(L) + 2P$, where $P = p \times z$ is the total number of free parameters for each fit, p is the number of free parameters for each model.

†The BIC is calculated as follows: $BIC = -2\ln(L) + P\ln(q)$, where q is the number of observations [q(Aggregated, KOR group) = 1920, q(Aggregated, CON group) = 1920, q(Individual, KOR group) = 1200, q(Individual, CON group) = 1520].

higher than in the full set of participants (KOR group: mean, 0.45; CON group: mean, 0.89). In the CON group, the excluded participants tended to have slightly higher recognition scores ($d' = 3.17$, $P_r = 0.82$); however, in the KOR group, the recognition scores were similar to the pre-exclusion group mean ($d' = 1.07$, $P_r = 0.17$). The excluded KOR participants did not appreciably differ from the pre-exclusion KOR group in terms of age (mean age, 49.33 years), NART-IQ score (mean score, 89.00), RBMT (mean score, 6.22), or education level (mean level, 4.11). Listwise deletion of these participants did not result in any qualitative changes in the recognition and priming differences reported, with the exception that the difference in the priming effects between the groups was only marginal ($t_{(32)} = 1.51$, $p = 0.07$, $d = 0.53$, one-tailed; KOR group: mean, 0.30; SE, 0.14; CON group: mean, 0.64; SE, 0.16); thus, there is need for a little caution in the claim of a deficit in priming in this KOR group. However, the priming effect in the KOR group subset ($d = 0.52$) was still smaller than that of that of the CON group ($d = 0.90$), and was only marginally significantly different from chance ($t_{(14)} = 2.09$, $p = 0.055$), which is, at least, still consistent with a deficit.

As predicted by the SS model (Prediction 2), in the KOR group, mean identification levels for items judged old were lower than those of items judged new within new and old items: ID(correct rejection) versus ID(false alarm): $t_{(14)} = 3.04$, $p = 0.009$, $d = 0.42$; ID(miss) vs ID(hit): $t_{(14)} = 3.98$, $p = 0.001$, $d = 0.74$ (Fig. 4b). Furthermore, as predicted by the SS model (Prediction 3), the magnitude of the priming effect for items judged new [calculated as ID(correct rejection) − ID(miss)] was significantly lower than the priming effect for items judged new in the KOR group ($t_{(14)} = 2.51$, $p = 0.025$, $d = 0.51$). However, the priming effect for items judged new was not reliable in this group ($t_{(14)} = 0.083$, $p = 0.94$, $d = 0.02$). Similar trends regarding Predictions 2 and 3 were evident in the CON group; however, these were not reliable (Fig. 4b): Prediction 2: ID(correct rejection) versus ID(false alarm), $t_{(18)} = 1.50$, $p = 0.15$, $d = 0.23$; ID(miss) versus ID(hit), $t_{(18)} = 1.29$, $p = 0.21$, $d = 0.15$; Prediction 3: $t_{(18)} = 1.18$, $p = 0.25$, $d = 0.28$. The priming effect for items judged new was, however, reliable in the CON group ($t_{(18)} = 2.89$, $p = 0.01$, $d = 0.29$). A 2 (item type: old, new) × 2 (judgment: old, new) × 2 (group: CON, KOR) ANOVA was also conducted on the identi-
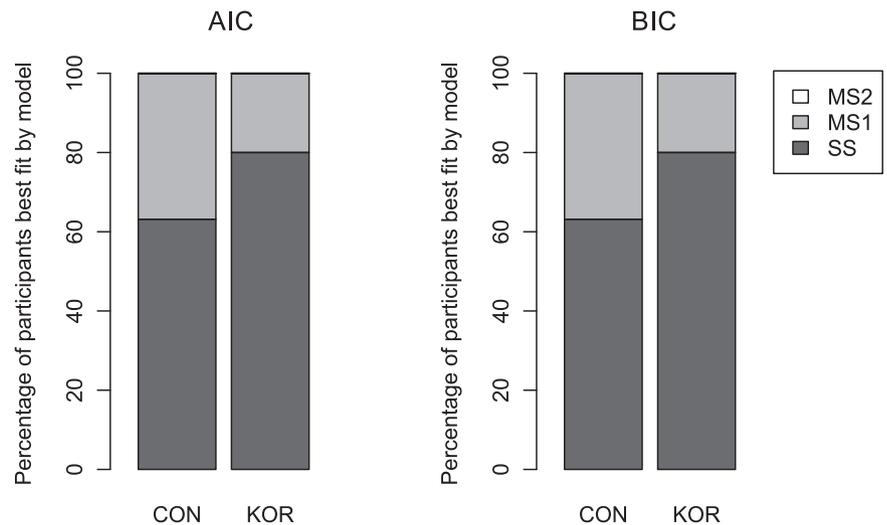
Figure 5. Model selection results. Each bar represents the percentage of participants best fit by each model according to the AIC and the BIC in the CON and KOR groups. The SS model was the best-fitting model for the majority of participants, with the remainder being best fit by the MS1 model.

fication levels. There was a significant main effect of judgment, $F_{(1,32)} = 21.23$, $p < 0.001$, $\eta_P^2 = 0.40$, indicating that identification levels tended to be lower for items judged old versus new. No other main effects or interactions were significant (main effect of item type: $F_{(1,32)} = 3.28$, $p = 0.08$; all other F values <2.33, p values >0.137, η_P^2 values <0.09).

Model fits

Table 2 shows the fit of the models to the data, and Table 1 shows the best-fitting parameter estimates of the SS, MS1, and MS2 models. When fit to the data aggregated across participants, the SS model provided the best fit to the CON group (indicated by the lowest AIC value in Table 2), but the MS2 model provided the best fit to the KOR group. However, the differences in AIC between the SS and MS2 models are very small (a difference of 1.2 for the CON group, and 0.3 for the KOR group), indicating that both models fit the data almost as well as each other (Burnham and Anderson, 2002). Furthermore, as shown in Table 1, the best-fitting value of w in the MS2 model was equal to 1, and the values of $\mu_{r|old}$ and $\mu_{p|old}$ were also very similar within groups, suggesting that the MS2 model fits the data best when it behaves more like the SS model. When the models were fit to each individual, the SS model provided the best fit to both groups (Table 2), and the AIC was substantially smaller for the SS model compared with the MS1 and MS2 models (i.e., >10), indicating substantial support for the SS model (Burnham and Anderson, 2002). The majority of participants
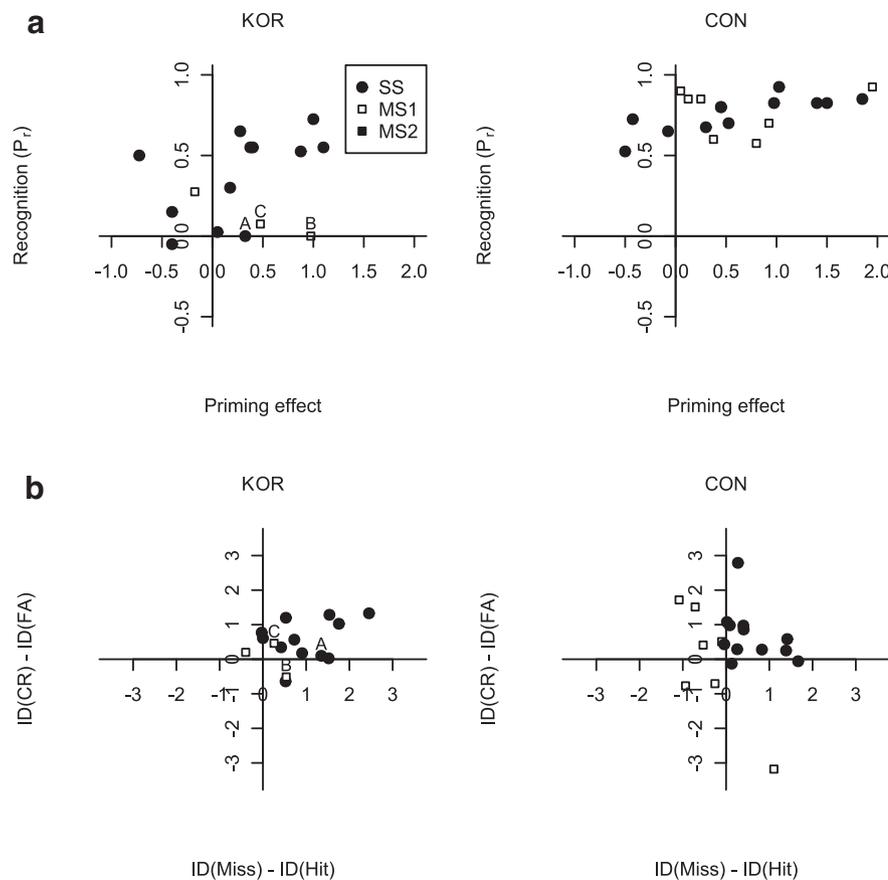
Figure 6. Best-fitting models for each participant (according to the AIC; individual level fits). **a, b,** The best fitting models are plotted according to P_r and priming (mean identification new − mean identification old) performance (**a**) and the difference in ID levels for items judged old and new (i.e., fluency effects) within old and new items (**b**). It is evident that the participants in the KOR group who were best fit by the MS1 model tended to show priming (or recognition) in the near absence of recognition (or priming). The MS1 model can reproduce such a pattern because the $\mu_{r|old}$ and $\mu_{p|old}$ parameters can vary independently of one another. In the CON group, there were also participants who were best fit by the MS1 model even though they showed relatively large positive recognition and priming effects. These participants tended to show an absence of fluency effects (or even a negative fluency effect) within old or new items (**b**, right). Because f_p and f_r are uncorrelated in the MS1 model, it does not predict fluency effects within old/new items. Thus, the participants best fit by the MS1 model appeared to exhibit results that were consistent with its predictions. The letters A, B, and C above the points in the KOR group label patients who showed priming effects despite performing very close to chance in recognition.

in each group were best fit by the SS model, with the remainder being best fit by the MS1 model (Fig. 5). The BIC results also tended to support the SS model (Table 2, Fig. 5).

The expected model results are indicated by the symbols in Figures 3 and 4. All models closely reproduced the key trends in the data: recognition and priming were lower in the KOR group than the CON group (Prediction 1); and the SS and MS2 models predicted nonzero differences between ID(correct rejection) and ID(false alarm), ID(miss) and ID(hit) (Prediction 2), and also between priming overall and for items judged new (Prediction 3; Fig. 4). The MS1 model did not, however, predict any of these differences (Fig. 4).

Data from individual patients who show normal priming despite a complete absence of recognition memory (e.g., patient E.P.; Hamann and Squire, 1997; Stefanacci et al., 2000; Conroy et al., 2005) is particularly challenging for single-system accounts (Berry et al., 2012). Three densely amnesic patients from this study who showed priming despite performing at/near chance in recognition yielded results that did not clearly provide evidence for any model, but it is important to stress that their results were

not incompatible with the SS model (Figs. 6, 7, patients A–C). Patient A was female, 51 years of age, with a NART-IQ score of 109, an RBMT score of 4, and an education level of 5; patient B was male, 54 years of age, with a NART-IQ score of 101, an RBMT score of 2, and an education level of 5; and patient C was male, 59 years of age, with a NART-IQ score of 87, an RBMT score of 12, and an education level of 2.

Patients B and C were best fit by the MS1 model, and patient A by the SS model (though the differences in AIC between the best-fitting models were small—<4). The mean priming effect in this subgroup was 0.59 (SE, 0.20), which is lower than the priming effect shown in the CON group (mean, 0.68; SE, 0.14), but still within the 95% confidence interval of the CON group mean (Fig. 4). From Figure 7, *a* and *b*, it is evident that the MS1 and MS2 models closely fit the recognition and priming results, whereas the SS model predicts a small amount of recognition in these patients, and a lower magnitude of priming than was evident in these individuals. From Figure 7, *b* and *c*, it is evident that (1) priming in patient A, but not patients in B and C, was below the lower 95% confidence interval of mean priming in the CON group; (2) all patients showed a fluency effect within old items, and patients A and C, but not patient B, showed a fluency effect within new items; and (3) patients A and B, but not patient C, showed a greater priming effect than the priming effect for items judged new. Thus, results 2 and 3, and to a lesser extent result 1, are largely compatible with the predictions of the SS model (and also the MS2 model). It is noteworthy that the SS model is able to reproduce a substantial priming effect in patient B despite very low recognition.

Discussion

Contrary to longstanding views that recognition memory and repetition priming are driven by distinct memory systems (Squire, 2009), this study showed that numerous results in amnesic patients could be predicted in advance by a single-system model: (1) reliable deficits in recognition and priming were found relative to the control subjects; (2) items judged old were identified at greater levels of fragmentation than items judged new within both old and new items; and (3) the magnitude of the priming effect overall was greater than the priming effect for items judged new (though note that priming for items judged new was not reliable in the KOR group). Findings 2 and 3 were not predicted by the MS1 model, but were reproduced by the MS2 model. The AIC and BIC model evidence measures, however, indicated that there was greater support for the SS model than the MS2 model. Thus, overall, the data from the amnesic patients favored the SS model over the MS1 and MS2 models.

Findings 2 and 3 are therefore in agreement with a previous study that found similar results in normal adults (Berry et al., 2012).

The deficit in priming found in the KOR group in this study contrasts with the widely held view that priming is preserved in amnesia. Although priming is frequently found to be preserved in amnesia (Gabrieli, 1998), many studies, like ours, have also reported deficits (Warrington and Weiskrantz, 1968; Cermak et al., 1993; Verfaellie et al., 1996; Ostergaard, 1999; Verfaellie and Cermak, 1999; Meier et al., 2009). When Korsakoff patients are specifically considered, priming deficits are often reported when the priming task is picture fragment completion (Hayes et al., 2012). There are different interpretations of such priming deficits. In KS, one account is that they reflect visuoperceptual impairments (Hayes et al., 2012). However, such an account does not appear to explain the priming deficit found in this study because baseline levels of identification (fragment identification levels for new items) did not differ between the KOR and CON groups, suggesting that the visuoperceptual abilities of the groups were appropriately matched.

Figure 7. Performance of the KOR group patients A, B, and C (as labeled in Figs. 3c, 6). *a–c*, Recognition (*a*), priming (*b*), and differences (*c*) in ID levels for items judged new and old within old and new items (i.e., fluency effects), and differences in the priming effect (overall) and the priming effect of items judged new (Predictions 2 and 3 of the SS model). Bars denote data, and symbols indicate the expected result from each model when fit to the data from each individual. The dashed lines in *a* and *b* indicate the lower 95% confidence interval for the mean recognition and priming performance, respectively, in the CON group (Fig. 4).

One possible multiple-systems interpretation of the deficit in priming is that priming is greater in the CON group because these individuals use their greater capacity for explicit memory to retrieve studied items from memory during the identification portion of a trial; doing so increases the magnitude of priming relative to the amnesic patients (Squire et al., 1985). Although possible, there is evidence to suggest that such an account is unlikely to apply to our data. For example, this type of explicit contamination of fragment identification performance is deemed more likely to occur (and be more effective) when participants identify fragments at both study and test. Under these conditions, an association between the fragment and the picture name can be formed during the study phase and then be recalled during the test phase (Verfaellie et al., 1996). In our study, however, participants only identified fragments during the test phase, so there was no opportunity for specific fragment–picture name associations to be formed during the study phase. Moreover, in experiments using a CID-R task with normal adults, it has been found that even under conditions that appear optimal for using an explicit retrieval strategy in a CID-R task (i.e., informing the participant whether the upcoming trial will contain an old or new item), there was no evidence of greater priming than under typical testing conditions (Ward et al., 2013; for a similar finding, see also Brown et al., 1991; for a discussion of explicit contamination in a similar task, see also Ostergaard, 1998, 1999).

The SS model explains the deficits in the KOR group as arising from the weaker strength of a single underlying memory signal for studied items relative to the CON group. Interestingly, the effect of KS was larger on recognition than on priming (Cohen's *d*: recognition, 2.69; priming, 0.53), and this was captured by the SS model (Cohen's *d*: recognition, 2.27; priming, 0.51). The SS model is able to predict this interaction because there is not a 1:1 mapping between strength and performance; the signal is scaled

differently and is subjected to different sources of noise for each task. That a single memory strength signal is expressed differently in two tasks in the SS model is conceptually similar to other models in which a single underlying memory trace is accessed in different ways depending upon the retrieval process (Greve et al., 2010). The difference in effect sizes predicted by the SS model is one possible explanation for why deficits are more frequently found in recognition than priming in amnesia. Consistent with this is the finding that priming tasks are typically less reliable than recognition tasks (Buchner and Wippich, 2000); indeed, the reliability of the recognition and priming tasks in our study tended to confirm this (see Materials and Methods).

In the CON group, numerical trends were found in support of Predictions 2 and 3, but these were not reliable. This is most likely due to low power: the number of misses and false alarms in the CON group was relatively low (CON group: median, 5 misses, 2 false alarms; KOR group: median, 16 misses, 11 false alarms), and so the variability in identification levels for these responses was relatively high (Fig. 3c). Clear evidence of Predictions 2 and 3 in normal adults has, however, been found across three experiments by Berry et al. (2012) with normal adults. They used a greater number of stimuli than this study (72–150 vs 40 old/new items), and overall levels of recognition were lower (*d'* values <1.5 vs 2.64), which resulted in more false alarms and misses.

One potential concern with the CID-R task is that the identification portion of the trial may affect the recognition judgment. This may be deemed likely since recognition and priming trials are necessarily interleaved due to the nature of the task. Early dual-process theories of recognition proposed that perceptual fluency can act as one basis of recognition (Mandler, 1980; Jacoby and Dallas, 1981), and studies have shown that the probability of an old judgment to an item is greater if the rate at which it clarifies from a mask is fast rather than slow (Johnston et al., 1991). In

other words, a relatively fluent identification can be attributed to prior exposure. It is therefore possible that the relations between priming and recognition that we find are accentuated by the CID-R task. However, there is evidence from similar studies that have used blocked designs, which demonstrate that the within-item recognition-priming measure associations of the kind observed in this study are not dependent upon the interleaved nature of the CID-R task (Ostergaard, 1998; Sheldon and Moscovitch, 2010; see also discussion in Berry et al., 2012).

An important question is whether the SS model extends to other explicit tasks that are more reliant upon recollection (i.e., remembering prior context). Berry et al. (2012) found some evidence for this using a modified CID-R task with remember–know judgments (Tulving, 1985). Remember judgments are widely thought to measure a recollection memory process (Yonelinas, 2002). Berry et al. (2012) found that identification response times to items given remember judgments were faster than for those given know judgments (commonly thought to measure a familiarity process), and this was predicted by the SS model. In future research, it will be important to determine whether the model extends to other tasks that are reliant upon recollection such as source memory.

Finally, a remaining issue is whether the SS model can explain the kind of dissociation that is opposite to that reported in amnesia, namely, evidence of brain regions that support priming but not recognition. Although initial neuropsychological studies indicated that the right occipital lobe was such a region (Gabrieli et al., 1995), subsequent investigations have not corroborated this (Yonelinas et al., 2001; Kroll et al., 2003). Nevertheless, it is clear that regions outside the medial temporal lobe are involved in priming (and also recognition; Schacter et al., 2007), and one avenue for future research will be to determine how the activity of different regions maps onto the single strength signal in the SS model.

To conclude, the results from amnesic patients supported the predictions of the SS model. Numerous results were inconsistent with the MS1 model; this suggests that recognition and priming are not driven by completely independent explicit and implicit memory signals. Like the SS model, the MS2 model could account for the data. The MS2 model explains the deficits in recognition and priming in amnesia as reductions in the strength of both the explicit and implicit memory signals. There is also a substantial degree of association between the explicit and implicit memory strengths of a given item according to this model. The SS model, however, tended to be preferred according to model evidence measures and could predict the majority of results in amnesia in advance. Thus, the SS model appears to provide the most parsimonious account for the pattern of recognition and priming in amnesia found in this study.

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