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Citation for final published version:

Morey, Candice , Rhodes, Stephen and Cowan, Nelson 2019. Sensory-motor integration and brain lesions: Progress toward explaining domainspecific phenomena within domain-general working memory. *Cortex* 112 , pp. 149-161.
10.1016/j.cortex.2018.11.030

Publishers page: <https://doi.org/10.1016/j.cortex.2018.11.030>

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Author-final version of manuscript accepted for publication in *Cortex*, 30 November 2018

Sensory-motor integration and brain lesions: Progress toward explaining domain-specific phenomena within domain-general working memory

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Abstract

Reports of rare patients who seem to lack the ability to retain certain types of information across brief delays have long sustained the popular idea that newly-perceived verbal, visual, and spatial information is initially recorded in separate, specialized short-term memory buffers. However, evidence from these same cases includes puzzling details that question explanations based on isolated deficits to a specialized storage system. We highlight consistent findings from patients with deficient auditory short-term memory that warrant further investigation and may challenge the specialized store account, including that short-term recognition memory performance appears to be much stronger than recall, and not so obviously impaired. We also describe the substantial problems for the broader memory system caused by assuming that the patients' deficits are focused in a specialized module. We suggest that a sensory-motor integration account of the patient cases may adequately explain these patterns, and therefore presents a path toward incorporating into the embedded processes framework greater clarity about how domain-specific phenomena in immediate memory tasks arise. We further contend that applying ideas about sensory-motor recruitment could improve working memory theory.

Word count: 179

Sensory-motor integration and brain lesions: Progress toward explaining domain-specific phenomena within domain-general working memory

One of the biggest tensions between models of working memory arises from how best to explain the robust and consistent modality- and domain-specific phenomena observed in working memory tasks. Performing two tasks that both depend on verbal representations or that both depend on visual-spatial representations results in poorer performance than performing two tasks relying on a mixture of representations (e.g., Fougne & Marois, 2011; Fougne, Zughni, Godwin, & Marois, 2015; Logie, Zucco, & Baddeley, 1990; Thalmann & Oberauer, 2017). At the same time, there also appears to be a general limit that applies regardless of representation domain (Cowan, 2001; Cowan & Morey, 2007; Cowan, Saults, & Blume, 2014; Saults & Cowan, 2007; Vergauwe, Barrouillet, & Camos, 2010), which is incompatible with a simplistic model (which perhaps nobody endorses) in which there is one store for aural-verbal materials and a completely separate store for visual-spatial materials. It is clear that a model of working memory must be able to explain within-domain interference, but the multiple ways of accounting for this interference must be assessed. Some models claim to account for both within-domain interference in working memory and across-domain capacity limits without postulating the existence of domain-specific stores (Cowan, 2005; Cowan, 1988; Oberauer, 2013), but specialized short-term memory stores remain a prominent feature of many popular theories (Baddeley, 2012; Logie, 2011). We consider whether evidence from patients with selective impairments on certain kinds of short-term memory tasks adjudicate between these classes of working memory model.

Special attention must be given to evidence from brain lesions, which has been important in developing models of working memory that include specialized short-term storage. Theorists favoring the existence of domain-specific stores (e.g., Baddeley, 2012; Logie, 2011) rely more heavily on patient lesion data to justify postulating these stores, whereas theorists who refrain from including domain-specific short-term stores sometimes have been accused of ignoring this important source of evidence (but see Cowan, 1988, p. 182). Below, we briefly review competing accounts of within-domain interference and then re-examine these crucial data from patients with deficits on aural-verbal short-term memory tasks, considering how this evidence constrains any model that aims to explain short-term memory phenomena. Our re-consideration of evidence from the patient cases leads us to question the conclusion that a specialized short-term store is deficient in these cases, and to consider how the sensory-motor integration account (Buchsbaum et al., 2011; Buchsbaum & D'Esposito, 2008) and sensory-motor recruitment explanations of short-term memory more generally (D'Esposito & Postle, 2015) might be used to better incorporate domain-specific predictions into the domain-general embedded process working memory model (Cowan, 2005). The sensory-motor integration account of these patients is one in which their key neuropsychological deficit is in the ability to translate an auditory verbal representation into a motor sequence for recall.

1. Competing accounts of within-domain interference

The greater amount of interference between items from the same domain (e.g., two visual or two verbal items as opposed to one of each) is undeniable but has been explained by several different theoretical approaches. Some have assumed that there are many kinds of feature-detecting mechanisms in the brain and that representations from

the same domain have more neural overlap and therefore interfere more with each other than with representations from other domains (e.g., Cowan, 1988; for a development of the functional definition of such interference see Oberauer, Farrell, Jarrold, & Lewandowsky, 2016). In the embedded processes framework, general costs to holding information in the focus of attention arise from the need to periodically maintain the activation of long-term memories currently supporting the task (Rhodes & Cowan, 2018). Others assume that interference takes place not during storage but during perception and that short-term memory phenomena are actually byproducts of perceptual affordances rather than the structure of a memory system (e.g., Macken, Taylor, & Jones, 2015). Similarly, the ability to link sensory representations to motor processes has been of interest (Buchsbaum & D'Esposito, 2008; Caplan, Waters, & Howard, 2012). One popular view, however, posits specialized mnemonic structures for storing or rehearsing representations in different domains separately (e.g., Baddeley, 2012; Barrouillet & Camos, 2015; Logie, 2011).

The multiple-component model of working memory (Baddeley, 2012) includes both domain-specific and domain-general aspects. The model includes specialized stores for verbal and visual-spatial information, and also allows an amodal episodic buffer to represent information that cannot be represented elsewhere (such as semantic information and binding between visual and verbal features). At first glance, this conception seems to provide an adequate account of the consistent empirical findings in the short-term memory literature by allowing for both domain-general and domain-specific representation. However, empirical challenges to the assumption of separate stores suggest that alternative accounts should be considered. Findings of common limits on temporary storage (C. Morey, Cowan, Morey, & Rouder, 2011; Sauls & Cowan,

2007; Vergauwe et al., 2010) pose one challenge to this view. If verbal and visuo-spatial information could be held separately by two buffers, there should be no interference between modalities provided that the perceptual intake of the stimuli is not overloaded, and in the above research it has not been (e.g., stimuli in the two domains have been presented one at a time). This challenge may possibly be accommodated by the assumption of domain-general along with domain-specific storage resources, as explicitly introduced by Baddeley (2000). However, it has also been shown that many classic patterns consistent with the assumption of an aural-verbal short-term store may be attributable to perceptual (e.g., Hughes, Marsh, & Jones, 2009; Jones, Hughes, & Macken, 2006) or linguistic phenomena (Jalbert, Neath, Bireta, & Surprenant, 2011; Majerus, 2009; Schweppe, Grice, & Rummer, 2011). Such findings directly challenge the need to assume specialized storage at all. Interpretation of the neuropsychological evidence that injury can lead to a focal impairment in immediately recalling aurally-presented verbal information is therefore important for determining whether we need to assume a specialized phonological short-term memory component.

2. Interpreting neuropsychological data

Whenever experimental evidence appears to falsify hypotheses about short-term stores, patient cases are brought forward as “smoking-gun evidence” for short-term stores, meaning that the evidence points too strongly towards distinct short-term stores for a reasonable person to doubt that interpretation, and therefore any apparently contradictory experimental evidence should be reconsidered or disregarded (Gathercole, 1994; Logie, 2011). Neuropsychological evidence thus plays an enormous role in this theoretical debate, so it is important to establish whether the characterization of these impairments as short-term storage deficits is truly undeniable. Alternative hypotheses

suggest instead that the deficits to short-term recall exhibited by these patients might arise from selective impairments to the speech production system (Caplan, Waters, & Howard, 2012), to rapid and perhaps selective decay of phonological activations within a linguistic-semantic network (Martin & Saffran, 1992), or to the ability to link aural sensory representations with speech production processes (Buchsbaum & D'Esposito, 2008). These suggestions, when united with an amodal storage system such as that in the embedded processes framework (e.g. Cowan, 2005), might present a plausible solution to the tension created by evidence that short-term memory is apparently both domain-specific and domain-general. Specifically, as we outline in more detail later, any modality-specific benefits and limitations may be inherited by the memory system from perceptual and motor systems, whose specificity of function is much less ambiguous, while amodal working memory itself imposes further limits that arise during performance of immediate memory tasks. Explicitly predicting that memories are influenced by the specialized capabilities of modality-specific perceptual and motor systems allows a path for an amodal memory system to express further specificity. Furthermore, in contrast to positing many distinct temporary memory stores, this route to resolving the tension between generality and specificity in working memory has the additional benefit of parsimoniously reducing redundancy across interrelated cognitive systems.

The defining characteristic of the aural-verbal short-term memory deficit is poorer performance recalling sequences of verbal materials when the information is aurally rather than visually presented. This unusual pattern is striking when compared with the performance of healthy controls for several reasons. First, the ability to compare recall of the very same memoranda (e.g., lists of digits, letters, words, etc.),

differing only by mode of acquisition, is powerful. Second, healthy individuals not only show consistently longer memory spans than these patients, but show the *reverse* pattern with respect to modality. The patients' recall of visually-presented information exceeds that of aurally-presented information, whereas typically, recall is superior for aurally-presented verbal materials than for written text (Penney, 1989). Furthermore, both in patients like KF and PV (Basso, Spinnler, Vallar, & Zanobio, 1982; Warrington & Shallice, 1969), who are believed to present with relatively pure aural-verbal short-term memory deficits, and in conduction aphasia (which frequently includes aural-verbal short-term memory deficits; Buchsbaum et al., 2011; Shallice & Warrington, 1977) more broadly, the deficit is not ameliorated by the opportunity to recall via pointing (Tzortzis & Albert, 1974; Warrington & Shallice, 1969). This confirms that the problem is not restricted to speech specifically, bolstering the view that it has something to do with memory. Furthermore, there is also evidence that these patients can learn novel aural-verbal sequences given sufficient time and repetition, which naturally focuses the deficit on recent, immediate memories. Altogether, this evidence has suggested to researchers that temporary storage of aurally-presented verbal information is sufficiently circumscribed and distinct from other mnemonic and linguistic processes that it may be specifically and selectively damaged.

We evaluate the evidence presented in case reports identified as aural-verbal short-term memory impairment and consider whether this evidence is strong enough to justify the theoretical weight it bears for multiple-component working memory theories. Is it necessary to interpret the case evidence as reflecting specialized short-term memory stores, or are the alternative interpretations that implicate sensory-motor integration also viable? We conclude that the limited evidence these cases present does

not unequivocally demand the supposition of specialized short-term memory stores. Considering the limited data available from short-term aural-verbal memory cases, our assessment reveals findings that are inconsistent with the argument that these patients suffered from a specialized storage deficit. Though we acknowledge that the existing neuropsychological evidence does not absolutely rule out the hypothesis that there is a specialized short-term store for aural-verbal information, we conclude that the data may be interpreted equally well under the sensory-motor integration account. We further consider whether assumptions arising from embedded-process style models of working memory (Cowan, 2005) can fill apparent gaps left by the view that short-term memory phenomena emerge from sensory-motor integration.

3. Weaknesses in the selective short-term storage account of neuropsychological patients

3.1 Impurity of the cases. Patients KF (Shallice & Warrington, 1970; Warrington, Logue, & Pratt, 1971; Warrington & Shallice, 1969), JB (Shallice & Butterworth, 1977; Warrington et al., 1971) and PV (Basso et al., 1982; Vallar & Baddeley, 1984) took part in a variety of tests, including tests of verbal short-term memory administered both aurally and visually with many kinds of verbal materials for a range of sequence lengths. These patients are often considered “pure” cases of aural-verbal short-term memory impairment because much of their language functioning was reportedly preserved. Even so, each of the complete case descriptions mentions other language disturbances occurring shortly after the injury and gradually improving, which is consistent with the conjecture of Buchsbaum and D’Esposito (2008) that these patients may have experienced greater facility from the right hemisphere in compensating for language dysfunctions, preventing them from presenting as typical

conduction aphasics. Furthermore, like conduction aphasics, they each experienced some sustained difficulty with word repetition. Patients with conduction aphasia also suffer from aural-verbal short-term memory deficit (Kinsbourne, 1972; Shallice & Butterworth, 1977; Shallice & Warrington, 1977; Strub & Gardner, 1974; Tzortzis & Albert, 1974), and are often considered alongside KF, JB, and PV despite their additional symptoms. One interpretation of this is that it is the patients' aural-verbal short-term memory deficit that causes problems with word repetition (Shallice & Warrington, 1977), but the reverse could also be true. It is clear that short-term memory spans and word processing indicators (e.g., word repetition) correlate strongly in these patients, such that patients with longer memory spans show less deficiency in phonological processing (Majerus, 2009). We consider the range of evidence presented by these patients, placing greatest weight on the data from KF, JB, and PV.

3.2 Response-based inconsistencies. Despite the consistent immediate recall deficits these cases present, some evidence provided within these case descriptions poses challenges for the idea that a short-term memory store is impaired. One problem for this hypothesis is that their recognition memory appears to be much better than their spoken recall. The patients' ability to recognize more than they could recall makes it difficult to disentangle some component of speech production or motor planning from storage, and muddies estimates of how deficient their ability to retain information across short delays really was. Some patients undertook whole-sequence matching tasks in which they heard an aural list, then heard another list and decided whether it was identical to the first or different by one item. We present data from this task taken from Warrington and Shallice's (1969) report of KF and from a report including three conduction aphasics (Tzortzis & Albert, 1974) in Figure 1. Less detailed,

but consistent evidence also comes from two patients described by Kinsbourne (1972), one of whom managed 80% correct with 4-digit lists and one of whom responded correctly to each of three 8-digit lists, and from patient LS, who performed 85-90% correct on a whole-sequence matching task comprising lists of three words (Strub & Gardner, 1974). Referring to the data plotted in Figure 1, KF's recognition performance is not only far superior to his recall performance, but not even obviously impaired. Note that KF is the only "pure" case of short-term memory deficiency in this set, but his recognition boost is, if anything, more pronounced than that of the conduction aphasics. Warrington and Shallice used KF's intact performance on matching sequences of as many as four items to argue that KF's auditory perception was undamaged. However, this sequence matching task is analogous to the recognition memory tasks widely used to estimate how much visual information participants can remember (e.g., Vogel, Woodman, & Luck, 2001; Wheeler & Treisman, 2002), and may be applied generally to cases in which the identification of a change in a set depends on consideration of the whole sequence (Rouder, Morey, Morey, & Cowan, 2011). It is thus not clear that patients like KF who could perform this comparison task well can be reasonably described as having selective damage to a short-term store.

FIGURE 1 HERE

To begin to quantify the difference between recognition and recall in these patients using the very limited information available, we attempted to estimate the number of items (k) they maintained on these tasks. For the recognition data, we applied Pashler's (1988) method for estimating k . For the recall data, both proportions of whole sequences recalled as well as proportions of items from those sequences (i.e. including partially correct sequences) are reported so we produced separate k estimates

from both. Additional details about how these estimates were derived are available in our supplementary materials (<https://osf.io/wbmk7/>). These three values for each patient are given in Table 1. Along with the proportions correct reported in the papers and reproduced in Figure 1, these values suggest that the patients, particularly KF, were capable of maintaining more information than their recall performance suggests. This is especially striking when we consider KF only attempted 4-item lists on the whole-sequence matching task which informed our recognition-based k . Capacity estimates are naturally constrained by the maximum size of the set the participant attempted. Given the opportunity to attempt longer lists in the recognition task, KF's k value would likely have been even higher. It is worth emphasizing that performance of this recognition task required accurate serial order memory to not reject intact sequences as changed as well as to identify the changed item in the list. Recall, on the other hand, poses the additional demand of *producing* the sequence.

Ideally, we would be able to compare the performance of the patients on whole display matching to performance of healthy participants, but no data from comparable healthy participants on this exact task are available in any of the case reports (though some data from patients with other deficits, who performed near ceiling, are available; Tzortzis and Albert, 1974). One way to assess recognition failure is to compare performance with what would be expected if the participant were guessing (i.e., 50%). By this standard, most of the patients tested demonstrate memory for these lists up to at least 4 items (which was the maximum tested in most cases; exceptions noted above). Our estimates of the number of items in memory are in agreement with this observation; with the exception of CS1, the patients appear to retain the majority of the presented sequences up to 4-items long. Nevertheless, with a 50% chance of guessing

the correct response, it could be argued that relying on this task alone might overestimate patients' memory abilities (Shallice & Warrington, 1977). However, this critique applies equally to the task's use as a test of aural perception. One cannot say that strong performance on this task proves there was no perceptual deficiency and then assert that the same strong performance is uninterpretable if used to assess recognition memory. If we consider these patients' performance unimpaired, we must doubt the extent of these patients' memory deficiencies. If we consider performance to be impaired, then we must question the original interpretation of these data, which was that the patients' aural perception was unimpaired. Either way, this ambiguity throws the idea that an aural short-term store has sustained damage into doubt.

Shallice and Warrington (1977) re-examined recognition memory in KF and JB by devising a probe-recognition test in which the patients indicated whether a given item was present in a list or not. Using this task they report that KF made 35% errors on a 5-item list and that JB made 37% errors on a 6-item list. They stressed that this reflected abnormal recognition because these were high proportions of errors on list lengths below normal span. Although we have no data from a comparison control sample, these error rates do strike us as rather higher than would be plausible in healthy individuals, but this is difficult to say without appropriate comparison evidence. Two reports with similar (but not identical) tasks in healthy young adults provide some evidence of how well control participants might have performed. Morey et al. (2013) measured performance on a verbal cued-probe task with aurally-presented 3- and 6-digit lists. Participants heard a digit list and later saw placeholders indicating positions in the list, with a digit in one of them. Their task was to say whether that digit was in that position. Participants performed well, but not perfectly, on 3-item lists (~3% errors

with the shortest measured retention interval, 4500 ms) and committed ~21% errors with 6-item lists. Baddeley, Chincotta, Stafford, and Turk (2002) administered whole-sequence matching tasks with series of 5-8 short or long words. Focusing on the short-word data (because they are more comparable to digits or letters), performance ranged from ~13% errors with 5-word lists to 40% errors with 8-item lists. Given the variability reported in these samples of healthy individuals on comparable recognition tasks, we cannot clearly rule out that the patients' recognition performance lies within one standard deviation of that of healthy participants. These data sources are not perfect comparisons for KF and JB: the tasks are not exactly the same, and the healthy samples are of course not appropriately matched. But these data demonstrate that even healthy young participants commit errors on verbal recognition tasks within "normal" span lengths. Judging whether patients' recognition data is as strikingly abnormal as their recall data is not straightforward. In light of these patients' spectacularly poor recall of much shorter aural-verbal lists than they could recognize, the recognition data at least suggest that the patients remember more aural-verbal information than their recall performance indicates. Though this degree of successful recognition may be outside a normal range, patients' comparative success recognizing longer lists than they could explicitly recall should be considered when determining the nature of their deficit, and evidence from matched control participants is badly needed.

3.3 Stimulus-based inconsistencies. Another puzzling finding from both KF and PV (plus some conduction aphasics; Tzortzis & Albert, 1974) is that they apparently show much less of an aural-verbal recall deficit when tested with digits rather than letters. We plotted data from KF (Warrington & Shallice, 1969), JB, WF (Warrington et al., 1971), and PV (Basso et al., 1982) when tested with digits and letters by mode of

presentation in Figure 2. This plot shows that with aural presentation, the patients performed substantially better when recalling digits than when recalling letters.

FIGURE 2 HERE

This pattern is unexpected from patients with a short-term phonological storage deficit for several reasons. If these patients lack access to a phonological store, then any kind of aural-verbal information should equally lack access. Assuming they have access to an impaired phonological short-term store, we presume that they can hold some amount of information, but assuming equal phoneme durations, they should recall the same number of phonemes no matter what category the phonemes are drawn from. In English (KF's language), most digit and letter names are single-syllable phonemes, so there is no reason to assume that letters would necessarily require more space in a phonological short-term store than digits. However, for Italian-speaking PV, one might have reasonably expected the reverse: In Italian, most of the digit names are multi-syllabic whereas Italian letter names mostly comprise only one syllable. Yet PV also shows an advantage for digits over letters with aural presentation, which shows that PV's performance reflects more than how many phoneme units she can hold in an impaired phonological short-term store. A potentially important advantage of digits over letters in either language is that they come from a smaller set. The sensory-motor interpretation of these patient cases presumes that their deficit arises from a breakdown in communication between the aural perception and motor production systems, which can be posited without presuming that the information is ever transferred to a specialized short-term store (Buchsbaum et al., 2011; Buchsbaum & D'Esposito, 2008). Patients with this deficiency in planning responses would plausibly benefit from restriction of the response choice set, as healthy individuals do.

In light of the all of the other evidence of short-term memory deficits, it might be tempting to suppose that better memory for digits than letters is evidence of KF and PV relying on their intact long-term learning to somehow “hack” these immediate recall tasks (as suggested of patient IL by Saffran & Marin, 1975). While this may be plausible, it is unsatisfying as a unique explanation of patient’s deficient performance because similar patterns are also consistently observed in healthy individuals (refer to the literature review and original data of Jones & Macken, 2015). To demonstrate that patients are compensating by relying on a different memory resource, one must show that they perform the unusual strategy to a greater extent than healthy individuals do. Because we do not have appropriate comparison data to consider this, we have no reason to believe that these patients rely on long-term knowledge to assist aural-verbal recall to an unusual degree. While this pattern could probably be explained in some way by invoking the interaction of multiple working memory components, better recall from a more restricted set of choices is likewise consistent with the suggestion of a deficit in integrating aural perception with response planning. Though the digits > letters pattern does not allow us to clearly distinguish the best account of poor short-term memory performance, it is sufficiently consistent to be considered further in theoretical predictions about how a patient with a damaged memory store or a damaged ability to integrate sensory representations with response planning would be expected to deal with various sets of materials.

While contemporary models of multiple-component working memory acknowledge that short- and long-term storage must interact somehow (Baddeley, 2012; Logie, 2011), they do not explicitly posit a clear method for how this interaction takes place. This specificity is needed if we are to generate predictions for how damage to a

phonological short-term store might affect integration of the contents of phonological short-term memory with long-term knowledge. KF and PV's recall, while apparently deficient, still seems to operate along similar principles expected based on data from healthy individuals. In order to account for this normal performance pattern, long-term memory or response properties distinguishing digits from letters must link up with the phonological store. If the store is damaged, the account may also have to incorporate the possibility that these same memory or response properties also can link up with visual-spatial storage in a similar manner, and to our knowledge that possibility has not been explored or substantiated in detail. It is possible that a multiple-component framework that posits a specialized verbal short-term storage system in addition to a visual short-term storage system and capabilities to interface with long-term knowledge could account for these patterns, but to our knowledge there is no account of the multiple-component system that explains how the proposed modules interact. This is necessary for supporting a more complex interpretation of the case evidence that goes beyond the claim that the observed neuropsychological patterns arise because of damage to the phonological store.

3.4 Insufficient evidence for compensatory visualization strategies. It is a stretch for the multiple-component working memory theories to explain the complete patterns of evidence provided by these cases, upon which they have relied so heavily. According to those theories (e.g., Baddeley, 2012; Logie, 2011), both auditory and visual input of speech should be primarily processed by the phonological store. However, auditory input to that store is supposedly more automatic, whereas visual input supposedly makes its way into the store only with the help of covert articulation. Visual input of verbal memoranda can also benefit from visuo-spatial coding to some

degree. If it is the phonological store that is damaged and not, say, the auditory input to that store or the communication between auditory perception and motor planning, then the pattern of patient evidence can be explained only by the suggestion that patients lean heavily and somewhat successfully on visuo-spatial storage for printed language.

However, the available evidence provides rather little reason to suppose that aural short-term memory patients cope by adopting visualization strategies, and does not attempt to show that patients use such strategies more than healthy individuals do. The representation format of a memory can be assessed by examining confusion errors in recall (Conrad, 1964). If letters are represented aurally and encoded in a phonological store, then participants should err by recalling phonologically-similar letters, whereas if letters are represented orthographically, they should err by recalling visually-similar letters. One might expect that patients with a deficient phonological short-term store would preferentially represent phonological information orthographically, and therefore show more tendency to confuse visually-similar letters than healthy participants do. Warrington and Shallice (1972) examined phonological and visual confusion errors in KF's written recall of aurally- and visually-presented verbal sequences. They found no evidence that KF encoded aurally-presented letters visually, which is perfectly consistent with the assumption that KF had limited access to this information, and therefore visually-based confusions would not have been expected. With visual presentation, there was more evidence of visual than phonological confusion errors, but no comparable data from healthy control participants to attest to KF employing a visual strategy beyond what might be observed in healthy participants (Logie, Della Sala, Wynn, & Baddeley, 2000; Logie, Saito, Morita, Varma, & Norris, 2016), which is crucial. We cannot interpret KF's performance as reflecting compensation for impaired phonological

storage by relying on visual coding unless it can be shown that KF commits *more* visual confusions than a comparable healthy control participant would. Vallar and Baddeley (1984) showed that, unlike healthy participants, PV does not show phonological similarity effects with visually-presented materials. They argued that the clear absence of phonological similarity effects with visual presentation in PV was evidence that PV strategically avoided converting visual input into a phonological representation using her intact sub-vocal speech, thereby avoiding transferring it to the presumably deficient phonological store. However, there was no corresponding evidence that she maintained visual representations instead, which means we cannot really tell how PV used the hypothetical multiple-component system to cope. Altogether, these patterns confirm a deficit related to aural-verbal materials, but fall short of convincingly demonstrating the compensation that a multiple-component working memory model implies.

In summary, the data from these patient cases does not manifestly point to a selective aural-verbal short-term memory deficit. Many patients evince strong recognition memory performance with quantities of aural-verbal stimuli beyond their span as measured by recall. Even if their performance were shown to be impaired compared to healthy controls, this suggests at least a milder aural-verbal memory deficit than usually supposed. The advantage for digits compared to letters, which was observed in KF (Warrington & Shallice, 1969), several conduction aphasics (Saffran & Marin, 1975; Tzortzis & Albert, 1974; Vallar & Papagno, 2002; though see also LS of Strub & Gardner, 1974, who performed equivalently on digits and letters), and PV (Basso et al., 1982) may possibly be explained in terms of damage to a short-term phonological store, but must be supplemented with speculation about how the other components help the patient to exhibit patterns of performance seen in healthy

individuals (i.e. digits > letters). Currently the level of specification regarding the interaction between components is not detailed enough to support a particular interpretation. Moreover, alternative explanations for these patterns have not been ruled out. Rather than a short-term memory deficit that has knock-on effects on word repetition and comprehension of complex sentences for which word order changes the meaning, we cannot clearly rule out the reverse possibility, namely that a subtle deficit of motor production or planning, or communication between auditory perception and motor systems is selectively impacting performance on certain aural-verbal memory tasks (e.g. those involving recall). In order to further distinguish these possibilities, we shall consider the overarching memory system in which a phonological short-term memory store must be situated, and consider the plausibility of a temporary phonological store in context.

4. Systemic problems with the selective short-term storage assumption

Memories are, of course, not exclusively represented in verbal forms. Much of what we remember – for instance, spatial maps, the facial features of our acquaintances, and even the conjunctions of such non-verbal features with their verbal labels – could not be maintained in an exclusively phonological short-term memory store. When we propose that there is a memory store exclusively for phonological information, we must therefore also suppose there are memory stores specialized for other sorts of information. The classic multiple-component model of working memory dealt with this by assuming a corresponding visual-spatial short-term store (Baddeley, 1986). Though this plausibly accounts for the capacity to remember information with phonological, visual, and spatial features, we might arguably need comparable structures for other kinds of representation.

Cowan's (1999; 1988) lack of a commitment to specialized stores in his embedded processes model had to do with the concern that the taxonomy of stores would be unclear given the need for storage of such things as the locations of sounds, musical chords, touch sensations, smells, abstract ideas, and so on. Cowan talked about these possibilities by referring to the diverse set of currently activated features within the long-term memory system. Cowan (1999, p. 89) added the point that, to account for memory of the new associations that occur within stimulus sets (e.g., the serial positions of items in the list 1-3-1), there is rapid, new learning in the long-term memory system and this newly-learned information can still be in an activated state. Accomplishing a similar function within a more modular approach, Baddeley (2000) amended his model by assuming that unaccommodated memories fall within the purview of a catch-all store, the episodic buffer. In Cowan's conception, it is possible for diverse features to be active in long-term memory and also for a few of them to be integrated into objects in the focus of attention; in Baddeley's conception, in contrast, information may be held in its specialized store, or possibly also in the domain-general episodic buffer. The multiple-component view of working memory thus requires evidence for at least phonological and visuo-spatial specialized stores, whereas the embedded processes view may accommodate domain-specificity without postulating specialized short-term stores at all.

Once we commit to one specialized store, we need others; modularity constantly begets the need for more modules (Van Orden, Pennington, & Stone, 2001) without necessarily advancing explanation of how the system works as a whole. Let's assume for the sake of illustration that there are verbal and visual-spatial stores, as both classic and contemporary multiple-component working memory models suggest, and that these are

sufficient for temporarily representing most features. If patients showing deficits in aural-verbal short-term memory provide the unassailable evidence for assuming such a store, and if logically assuming such a store means there must be something similar for visual and spatial representations, then occasionally a patient must appear showing intact aural-verbal short-term memory but selectively impaired visual or spatial short-term memory. Although several cases have been nominated as demonstrating either selectively deficient spatial or visual short-term memory (Bonni et al., 2014; Carlesimo, Perri, Turriziani, Tomaiuolo, & Caltagirone, 2001; De Renzi & Nichelli, 1975; Hanley, Young, & Pearson, 1991; Lepore, Celentano, Conson, & Grossi, 2008; Luzzatti, Vecchi, Agazzi, Cesa-Bianchi, & Vergani, 1998; Ross, 1980; Wilson, Baddeley, & Young, 1999), none demonstrated a convincing selective impairment. Morey (2018) reviewed this literature in depth, and found that these patients frequently presented with additional cognitive deficits that could not easily be attributed to a visual or spatial short-term memory impairment, making it unclear whether their visual-spatial memory deficit *must* be due to selective damage to a visual-spatial short-term store. In some cases, close examination of the administration of the verbal, visual, and spatial memory tasks revealed that these tasks differed in aspects other than their stimulus modality, for instance, the response mode or constraints on response options. When these factors are controlled across presentation modalities in healthy individuals, the apparent differences between presentation modalities are greatly reduced (Ward, Avons, & Melling, 2005). Until similarly controlled procedures are adopted when comparing verbal with visual or spatial memory in patients, we cannot definitively diagnose the source of apparent dissociations in patients. This means that none of these cases present with the clear reverse of KF or PV's experience. None of them, when combined with the

evidence of KF or PV, provide us with an unambiguous double dissociation that can only be attributed damage or sparing of the temporary store specialized to maintain one specific kind of representation.

Possibly, as tests of visual and spatial memory become increasingly sophisticated, more convincing evidence from patients with selective deficits in spatial or visual memory will emerge. Future patients demonstrating short-term memory deficits might be tested even more extensively, and the results of these tests could eventually bolster hypotheses about specialized temporary stores. However, the logical problems created by assuming this modularity of function will remain. Acknowledging that short-term stores for verbal and visual-spatial maintenance are not sufficient, Baddeley (2000) now also includes amodal storage in the working memory model. Competing models of working memory also typically include some provision for amodal storage (Barrouillet & Camos, 2015; Cowan, 2005; Oberauer, 2013). If everyone assumes there is amodal temporary storage alongside domain-specific temporary storage, then double dissociations based on the presumed domain of the representation become impossible to interpret clearly. We would be unable to tell whether the component that seems to be intact is a domain-specific store specialized for holding the sort of information that the patient *can* recall, or whether the patient is relying on the amodal resource. Extensive testing with many kinds of materials targeting maintenance versus other processes would be needed to try to tease apart these possibilities. These problems multiply when we consider whether the functions in question belong to the memory system, the language system, or a perceptual system. At some point, we must consider whether such clearly interdependent activities like temporary memory for speech, aural perception, and planning output are related, how they may be related, and what redundancies there

may be in the separate frameworks we use to describe perception, language and memory.

Finally, others have noted that the loci of lesions that lead to auditory short-term memory impairments are inconsistent across patients (Buchsbaum & D'Esposito, 2008; Gordon, 1983). Of course, it could be the case that the precise locus of a phonological store differs per individual, or that in fact the construct of a phonological store is distributed across the brain. However, labeling a particular set of processes or phenomena a “store” implies certain properties which can be tested. For instance, the region or network of regions that we call a “store” should be exclusively used for storage of whatever sort of material it is meant to store, and should be in use during the retention period over which the material is demonstrably maintained. Buchsbaum and D'Esposito demonstrate that the most plausible overlapping loci for a phonological short-term store in healthy individuals are compromised because the same loci have been shown to be involved with storage of non-verbal information, or even with functions other than storage. If the regions reflecting a “store” do not behave consistently with our assumptions about what stores do, then it make sense to reconsider our assumptions. It is clearly problematic for the specialized store idea that no region or network of regions can yet be pinpointed that is both uniquely for temporary storage and also uniquely for representing information in a particular format.

In summary, suggesting that these patients' poor aural-verbal recall reflects a damaged aural-verbal short-term memory store presents as many puzzles as supposing that the defect to recall relates to a specific impairment of the language system, or the integration of aural perception with the planning of motor output. Even if we were to accept that the evidence *demand*s a specialized aural-verbal short-term memory store,

there has been no unambiguous double dissociation in which other patients show the reverse deficits with visual or spatial information without also presenting with unrelated difficulties. Furthermore, now that it is widely acknowledged that working memory includes domain-general storage, all of these apparent double dissociations must be reconsidered, because we can no longer map intact performance to a particular module. Positing more than two modular, specialized short-term memory stores demands parallel chains of evidence that have not yet emerged. The multiple-component models of working memory that have traditionally guided interpretation of these cases are challenged by models that can also account for the experimental evidence, and that allow the possibility of incorporating domain-specificity via systems other than short-term memory. Because the extant patient evidence may be interpreted in several distinct ways, this evidence does not yet compel models of working memory to include specialized short-term stores. We must acknowledge that we cannot measure memory in a perfect vacuum, and assume that measurements of memory always also depend on related systems. Whatever components or processes we assume, we must consider how much they overlap with the components of other cognitive systems.

5. Sensory-motor integration and modality-specific effects within an amodal working memory

Though backed up by considerable evidence (Buchsbaum et al., 2011; Buchsbaum & D'Esposito, 2008; D'Esposito & Postle, 2015), the sensory-motor integration account of short-term memory patient cases (and the sensory-motor recruitment interpretation of cognitive neuroscience evidence more generally) lacks the compelling simplicity and vividness of the classic multiple-component working memory model's temporary stores. However, we think that in combination with an amodal attentional view of the working

memory system, the sensory-motor integration account may be better fleshed out, and may ultimately prove to explain benchmark findings more thoroughly than the traditional multiple-component model. The embedded process model of working memory (Cowan, 2005) focuses on describing the amodal core of the working memory system, which presumably causes the persistent capacity limits observed both within and across stimulus domains (Cowan, 2001). The embedded process model posits that some memories are maintained at a heightened level of activation, including newly-learned episodic information. Although any number of features can be concurrently activated according to the theory, only a small number of them can be integrated together and concurrently held as objects, ideas, or events in the focus of attention. The activated features can come from environmental input including semantic features of attended events and sensory features of all events. They can also come from long-term memory through associative processing, or from items recently but no longer in the focus of attention. Importantly, there is no explicit requirement that the activated features be represented in a short-term store.

The sensory-motor integration account supposes that specialized perceptual and motor regions support memory functions, and indeed bring about the robust and consistent phenomena that classically distinguish “short-term” from “long-term” memories. This explanation is supported by evidence that overlapping regions and networks become active during memory, perception and, in some cases, motor performance (e.g., D’Esposito & Postle, 2015). In particular, there is a multivoxel pattern signature of specific activated items when they are needed for the current task (i.e., when they are in the focus of attention), with the activation occurring in the same general regions that process the information perceptually: primarily temporal cortex for

verbal items, occipital cortex for visual items, and with different specific subregions and patterns for bars, faces, words, etc. However, these regions subserve functions besides storage, and the activation associated with a specific type of item need not be continuous for successful memory retrieval to occur (Lewis-Peacock, et al. 2016), which makes them implausible substrates for specialized short-term memory stores. There is also a frontal-parietal network that includes activation in the intraparietal sulcus reflecting how many items are currently actively in focus, not containing a copy of the information per se but linking to each item as a hub with pointers to the items (Cowan et al., 2011; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Li, Christ, & Cowan, 2014; Majerus et al., 2016; Todd & Marois, 2004; Xu & Chun, 2006). The sensory-motor integration account of short-term memory phenomena is thus compatible with amodal models of working memory like the embedded process model (Cowan, 2005). In terms of the embedded processes model (Cowan, 1988, 1999, 2005), the activation of the information in cortical perceptual processing regions corresponds to the activated portion of long-term memory, and the indices of these objects in the intraparietal sulcus presumably form the core of the focus of attention.

This neural activation evidence helps to restrict what is encompassed in the breadth of activated long-term memory, suggesting that it need not encompass specialized temporary stores. In order to map the embedded process model onto the multiple component model of working memory, activated long-term memory could be allowed to include the contents of specialized short-term stores (Cowan, 1995; Cowan et al., 2014; Rhodes & Cowan, 2018). But one could instead consider activated long-term memories to include fleeting representations temporarily preserved by perceptual systems and information kept active by motor re-instantiation. Sensory-motor

recruitment makes it unnecessary to impose dedicated, specialized short-term “slave” systems into the embedded process framework’s activated memories: the activation of perceptual and motor systems can serve the memory system without creating redundancy.

One important complexity in the sensory-motor view that is not found in the multiple-component view is that it should be expected that representation quality is a combination of sensory-motor channels. For example, the printed word “smooth” relies on visual and orthographic analyses at first, phonological analysis derived from original acoustic experience, and a semantic analysis that comes from tactile experience. All of these feature types could serve as bases for working memory retention but also could serve as bases for confusions between stimuli. Multiple-component theorists agree that more than one store could hold an item (e.g., see Logie et al., 2000, indicating that there are not only phonological but also visual confusions between words) but the limited number of stores in multiple-component models cannot provide the richness of available sensory-motor processors. Further, there is the important open question for multiple-component theorists to address, namely how different storage components interact and pool their efforts to produce observed responses, which we raised earlier.

Allowing that an amodal working memory inherits such complexity from the sensory and motor systems themselves, without the further abstraction assumed when these signals are presumed to be converted to the contents of a specialized short-term memory store, also provides a path toward explaining modality-specific effects in short-term memory without resorting only to feature-based interference (which may occur across modalities, but is likely to be more prevalent when trying to remember information within a modality; see Oberauer, et al., 2016 for a description of this

possibility). The evidence provided by patients with selectively deficient aural-verbal recall cannot be elegantly explained by the general principle of feature-based interference, given their access to more information when probed via recognition. Incorporating the ideas of sensory-motor integration into the embedded processes approach allows the amodal storage system to express more domain specificity than feature-based interference allows. According to this view, the deficit of these patients is not in the storage of aural-verbal features, but in the translation of these sustained representations into a motor response. Applied more generally, we must presume that at least some of the robust, modality-specific phenomena observed in immediate memory tasks occurs because modality-specific limitations and benefits for various stimuli are inherited by working memory from activations of the sensory and motor systems; their very activation in these systems enables them to be recruited by the working memory system. We think that the patient evidence casts doubt on the idea that interference from overlapping or confusable features can fully account for the modality-specific phenomena observed in immediate memory, even though we also think the patient evidence falls short of unambiguously supporting modular short-term memory stores.

Another reason to prefer an amodal memory system that inherits the specializations of other systems over a dedicated multiple-component working memory system is that it neatly leads to explanations for why measured capacities of different kinds of information differ so drastically. Measured capacities for readily verbalizable information (e.g., letters, digits, words, nameable pictures) are consistently higher than capacities for visual or tonal information (e.g., Vergauwe et al., 2010) even when the visual memory task does not require memory for serial order (C. Morey, Morey, van der Reijden, & Holweg, 2013; Saults & Cowan, 2007), which may not be well-preserved

by the proposed visual-spatial short-term memory system (Logie, 1995). Strikingly, Vergauwe et al. (2010) observed higher spans for verbal materials even when accompanied by a high verbal cognitive load than they observed for spatial memoranda under the lowest cognitive load (whether verbal or spatial). Moreover, memories for verbalizable information are more resistant to interference (Morey & Mall, 2012; Morey et al., 2013) than comparable visual-spatial memories, even when the to-be-remembered verbal information is unfamiliar and not likely part of long-term knowledge (Morey & Miron, 2016). These memory phenomena mirror sensation phenomena: aural sensory memories persist longer than visual sensory memories (Cowan, 1988; Sperling, 1960), and there is no motor system for reproducing and communicating visual sensory information comparable to the language system, which can reproduce verbal information with high fidelity via speech. To account for these findings via dedicated short-term memory stores, one would need to specify a visual short-term memory system with a smaller capacity or limited precision, or explicitly restricted means for re-activating visual representations (or perhaps suggest that there is no specialized way to re-activate visual representations while there is a specialized way to reactive verbal information, as Barrouillet and Camos make explicit in their 2015 time-based resource sharing model), not one in which the dedicated visual short-term memory system includes storage and rehearsal components comparable to those of the verbal system (Logie et al., 2016). An advantage of assuming that an amodal memory system co-opts processes from other systems lies in its avoidance of redundancy across psychological phenomena. Because the perceptual and motor systems supporting verbal information versus abstract visual information differ, disparities in memory for these types of information can be better anticipated.

To reconcile an amodal account with neuropsychological deficits, Cowan (1988, p. 182), proposed that it is the control processes needed specifically for short-term memory that are damaged in patients with deficient short-term memory and preserved long-term memory. If these control processes are considered to apply to any short-term retention task, including recognition as well as recall, the evidence noted above of relatively preserved recognition would seem to contradict this alternative solution. However, some other interpretations of these control processes might make Cowan's suggestion indistinguishable from the sensory-motor account.

6. Concluding comments

There is a temptation to suggest that calling an immediate memory deficit a consequence of sensory-motor integration rather than selective damage to a short-term store is merely attaching a different name to the problem, which may do nothing to forward our understanding of the deficit or of memory system functioning more broadly (Shallice & Warrington, 1977). However, we think that reconsidering the source of the deficiency in these patients and acknowledging that the deficiency may not reflect damage to a dedicated memory system constitutes an important step forward in working memory theory. Theoretical debates in working memory are characterized by a constant tension between specialization and generality. A fundamental conundrum lies in how best to simultaneously explain two robust but apparently contradictory findings: 1) greater interference is observed between two tasks that involve representing information from the same modality than from representing information from different modalities (e.g., Fougne & Marois, 2011; Logie, Zucco, & Baddeley, 1990), yet 2) dual-task costs are observed even across modalities (Cowan & Morey, 2007; C. Morey et al., 2013; Vergauwe et al., 2010). Working memory is meant to describe the system that

integrates perceived information with long-term knowledge, and allows for the manipulation and transformation of memories. It is, by definition, a characterization of the junction of many functions, and must naturally incorporate their respective benefits and limitations.

We think that the evidence from aural-verbal short-term memory cases includes several clues that these patients' memories may function in some respects like a healthy individual's. These patients perform much better on recognition-based whole-sequence matching tasks than on recall tasks. They consistently perform better with information drawn from a more restricted set (e.g., digits rather than letters). Though PV shows poor memory for late-list items when recalling in serial order, she can recall the most recently presented items well if instructed to recall them first (Vallar & Papagno, 1986). These findings are not clearly predicted by the proposal that these rare patients simply represent less information in their damaged phonological short-term stores. By supposing that their impairments prevent normal sensory-motor integration from occurring but that a central, amodal memory system that draws upon sensory memories and motor affordances remains intact, we can explain their poor immediate recall performance by supposing that the memory system cannot commandeer one ancillary function which in healthy individuals boosts measured capacity.

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Table 1. Estimates of patients' capacity (k) based on their recognition and recall data.

	Recognition k	Sequence-correct k	Items-correct k
Case			
KF	3.00	1.80	1.30
CS1	1.00	0.94	0.92
CS2	3.00	2.77	1.82
CS3	3.00	2.84	2.45

Note. Details about how estimates were calculated are available online (<https://osf.io/wbmk7/>).

Figure 1

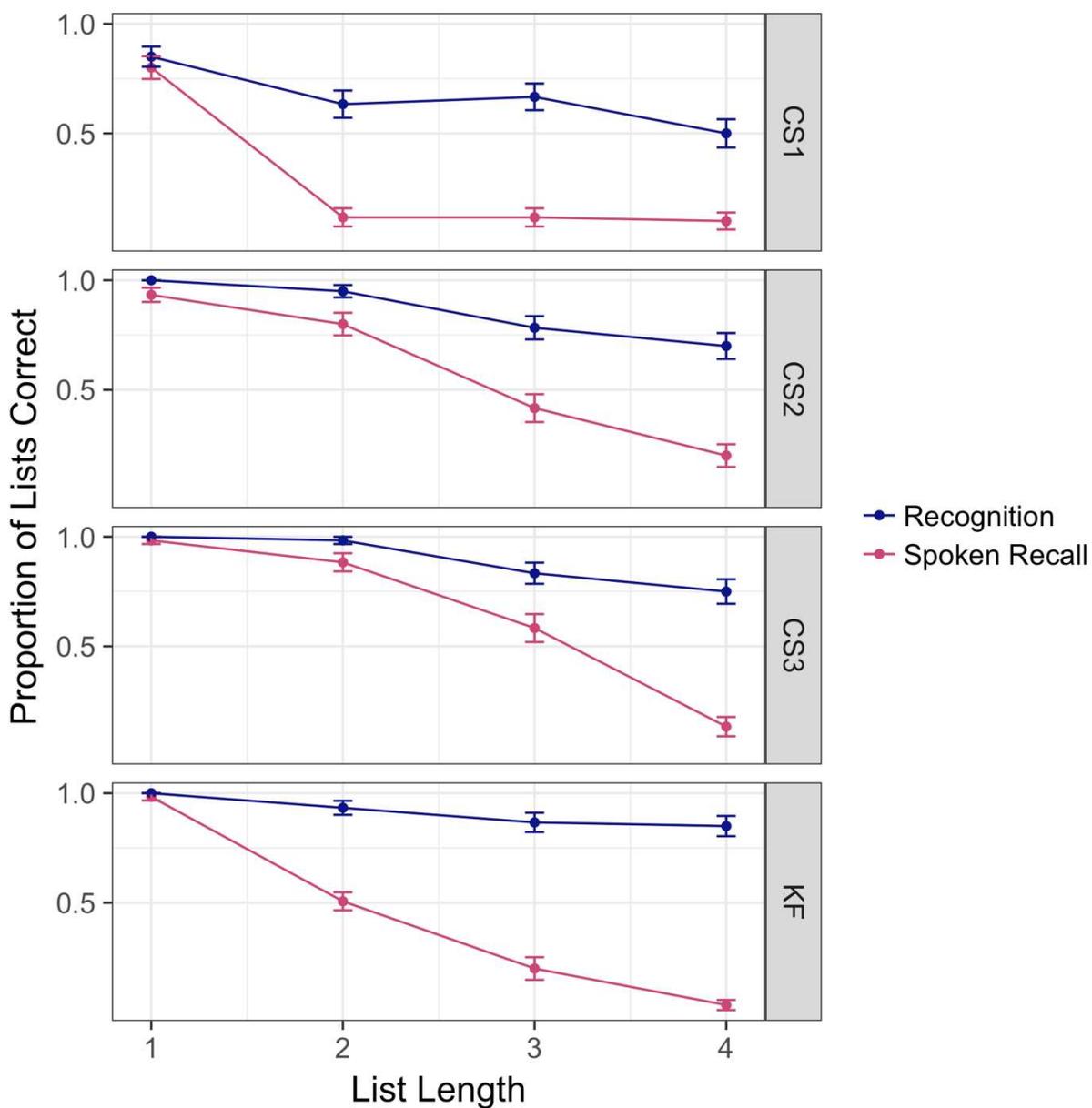


Figure 1. Proportions list-wise accuracy on spoken serial recall and whole-sequence recognition tasks with auditory stimulus presentation for KF (Warrington & Shallice, 1969, Tables 1-3) and three conduction aphasics (Tzortzis & Albert, 1974, Tables 1 and 6). Data include trials with digits, letters, and words as stimuli. Error bars are standard errors of the mean.

Figure 2

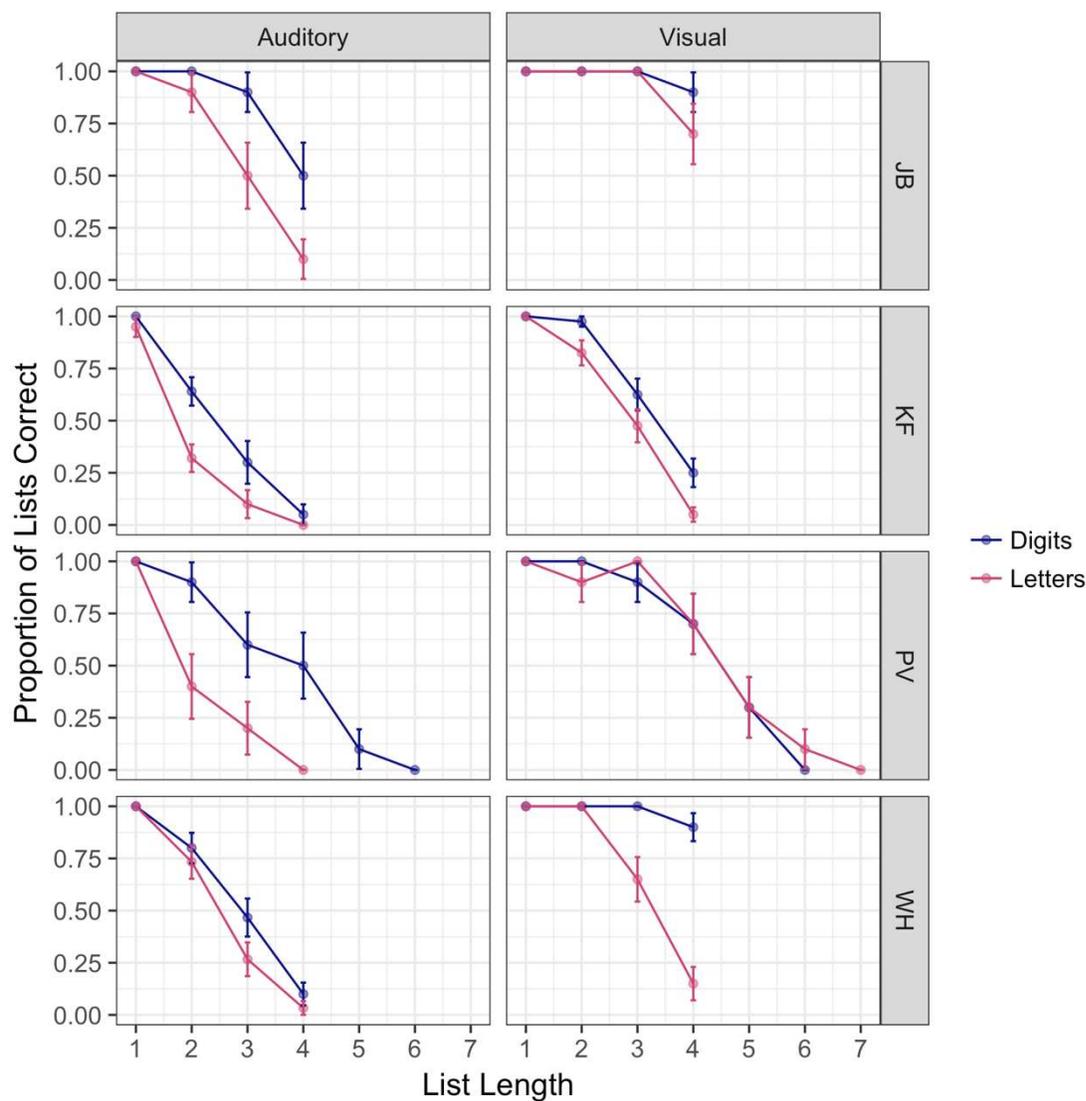


Figure 2. Proportions of lists recalled correctly (with standard errors of the mean) for patients JB, KF, PV, and WH with auditory and visual presentation, organized by list length and type of verbal material. Data for KF were taken from Warrington and Shallice (1969, Tables 1 and the 1-second presentation rate portion of Table 2); for JB and WH from Warrington, et al. (1971, Table 4 on p. 383) and for PV from Basso et al. (1982, Table 1).