Graded representations in behavioral dissociations

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Why do people sometimes seem to know things when they are tested in one way, while seeming unaware of this information when tested in a different way? Such task-dependent behaviors, or dissociations, often occur in infants and children, and in adults following brain damage. To explain these dissociations, researchers have posited separable knowledge systems that are differentially tapped by various tasks, develop at different rates and can be selectively impaired. There is an alternative account in which knowledge is viewed as graded in nature. Certain tasks tap weaker representations, while other tasks require stronger representations, leading to dissociations in behavior. The graded representations approach addresses dissociations observed in perception, attention, memory, executive functioning and language, and has implications for the organization, development and impairment of our cognitive systems.

Knowledge can be highly task dependent. We can simultaneously fail one test of knowledge while passing another test with flying colors. For example, people (with and without brain damage) can fail tests of memory for faces by being unable to remember the names for the faces, while nonetheless relearning the correct pairings of names and faces more quickly than incorrect pairings[1,2]. Adults with prefrontal damage and children might mistakenly follow old rules for how to behave rather than new rules, while nonetheless demonstrating verbally that they have learned the new rules[3,4]. And, people with dyslexia might seem to know more or less about words depending on the tasks used to test them[5].

Understanding such task-dependent behaviors, or dissociations, might be crucial to answering fundamental questions about the organization, development and impairment of our cognitive systems. This article explores these issues in the context of dissociations observed in perception, attention, memory, executive functioning and language.

In each domain, the prevalent approach explains dissociations in terms of separable knowledge systems that develop at different rates, can be selectively impaired, and contribute differentially to various tasks. A person might pass one task using one functioning system, but fail another task designed to measure the same knowledge because the separate system it taps is underdeveloped or impaired. An alternative approach explains dissociations in terms of knowledge representations that are graded, rather than simply being present or absent, with certain tasks requiring stronger representations. A person might pass one task using a weak representation, but fail another task designed to measure the same knowledge because it requires a stronger representation. At a conceptual level, representations can be graded in terms of how 'clean' they are for signaling the appropriate information, as opposed to being corrupted by noise or damage. At the neural level, representations can be graded in terms of the number of relevant neurons firing, their firing rates and the coherence of the firing patterns. The strength of representations depends upon various factors, such as the amount of environmental support for them, the state of development of an individual and the extent of neurological insult.

On the one hand, the graded representations alternative might seem obvious and not particularly worthy of review. After all, researchers have long been aware of the role that task difficulty might play in dissociations; graded representations could be viewed simply as the mechanism that underlies the effects of difficulty, with stronger representations needed for more difficult tasks. And, researchers have thought carefully about how even double dissociations (e.g. one group succeeding on task A but not task B; a second group succeeding on task B but not task A) need not imply the existence of separable underlying systems[6–9]. Thus, the separable systems approach might seem like a straw opponent. On the other hand, prevalent approaches to dissociations across a range of domains adopt the notion of separable systems and ignore the potential role of graded representations. Therefore, the graded representations approach warrants review. Furthermore, by providing a mechanistic basis for behavioral dissociations, the graded representations approach can inform thinking about cognitive systems beyond simply caching out notions of task difficulty.

Graded representations in perception

Individuals with optic aphasia have difficulty naming objects that are presented visually, despite being able to gesture the use of visually presented objects and name objects presented auditorally. Most accounts of these dissociations (reviewed in Ref. 10) assume that optic aphasia cannot result from damage to a basic system that converts visual representations into semantic (meaning) representations, and then semantic representations into representations for naming (Fig. 1). Based on

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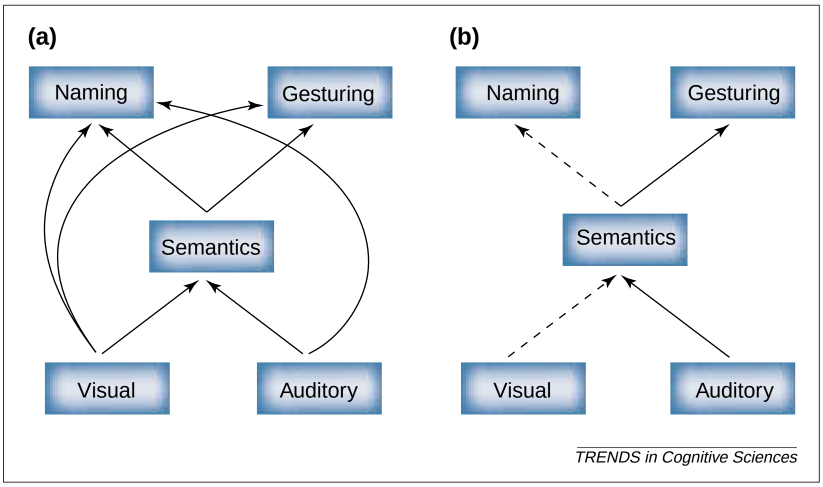

Fig. 1. Theories of dissociations observed in optic aphasia. According to prevalent accounts (a), the failure of individuals to name visually presented objects could not arise simply from damage to a basic system (indicated by straight arrows). Damage to the visual–semantics pathway is inconsistent with the ability of individuals to gesture the use of visually presented objects (which presumably occurs via the visual–semantic–gesture pathway); damage to the semantics–naming pathway is inconsistent with the ability of individuals to name objects presented auditorally (which presumably occurs via the auditory–semantics–naming pathway). Thus, additional systems must be posited (some of which are shown by curved arrows). According to a graded representations account (b), the observed dissociations could arise owing to partial damage to the visual–semantics and semantics–naming pathways in the basic system. The resulting weak representations most affect tasks that tap both damaged pathways, such as naming visually presented objects (which presumably occurs via the visual–semantics–naming pathway). Adapted, with permission, from Ref. 10.

this assumption, prevalent accounts must incorporate additional systems (in some cases via additional pathways) to the basic visual–semantic–naming system to explain the dissociations observed in optic aphasia.

In contrast, according to a graded representations account, these dissociations result from partial damage to both pathways in the basic visual–semantics–naming system[10]. Specifically, damage to the visual–semantics pathway could result in weak semantic representations for visually presented objects. These weak semantic representations might not be strong enough to drive a damaged semantics–naming pathway, leading to optic aphasics' difficulty in naming visually presented objects. However, these weak semantic representations might be sufficient to drive an intact semantics–gesture pathway, which allows optic aphasics to gesture the use of visually presented objects. Similarly, strong semantic representations (e.g. via an intact auditory–semantics pathway) might be sufficient to drive the damaged semantics–naming pathway, allowing optic aphasics to name auditorally presented objects. A neural network model that instantiates this graded representations account simulated the dissociations in optic aphasia[10]. Furthermore, the model predicted that individuals with optic aphasia should have more difficulty gesturing the use of visually presented objects than naming objects presented auditorally. The gesturing task leads to weak representations in the first stage of processing (visual–semantics) that are then propagated through the system, having a relatively large effect on performance, whereas the auditory naming task involves weak representations only at the end stage of processing (semantics–naming), resulting in relatively less impairment. This prediction is supported by several studies (reviewed in Ref. 10). The model also suggested a method for improving the performance of individuals by preventing them from responding to a visual object immediately. Such a delay improved the performance of the model dramatically, because weak representations from the visual–semantics pathway were strengthened before the semantics–naming pathway operated on them. This prediction has also been supported[11].

Graded representations in attention

Individuals with damage to parietal cortex tend to neglect the contralateral side of space, instead focusing attention on the ipsilateral side[12]. However, the evaluation of attention again depends crucially on how it is measured. Although individuals might be poor at identifying contralateral stimuli, they are able to make accurate same–different judgments about contralateral and ipsilateral stimuli[13,14]. The prevalent account of this dissociation was that the perception by the individual of the stimuli was preserved, but a separable system for conscious awareness of perception was selectively impaired. That is, individuals could attend to and perceive contralateral stimuli, but they could not achieve the conscious awareness of the stimuli required for identification[13].

In contrast, according to a graded representations account, the dissociation following parietal damage might result because less visual information (a weaker representation) is required for a same–different judgment than for identifying a stimulus[14]. This graded representations account predicted that: (1) neurologically intact participants should show the same dissociation with degraded stimuli (e.g. when the stimuli on one side of space are viewed through a diffusing mask); and (2) the dissociation should disappear in individuals with parietal damage and neurologically intact participants when the amount of visual information required for the two tasks is equated (e.g. with a forced choice procedure for the identification task). Both of these predictions were confirmed[14]. Furthermore, neural network models have demonstrated how graded activity patterns can govern attention, and how damage to such systems can lead to deficits observed in neglect[15,16].

Graded representations in memory

Some of the most compelling dissociations in memory occur early in development. For example, infants demonstrate an apparent memory for hidden objects within the first few months of life in violation-of-expectation studies[17,18], while

Box 1. Dissociations in memory development

Violation-of-expectation studies build on the assumption that infants look longer at events that they find novel or unnatural[a,b]. When the novelty or unnaturalness of such events arises based on objects that have been occluded, the longer looking times of infants at these events are taken as evidence of their memory for the hidden objects. Although these methods are not without controversy (e.g. see special issues covering debates on those methods in Refs c–e), they have provided important constraints on theories of memory development.

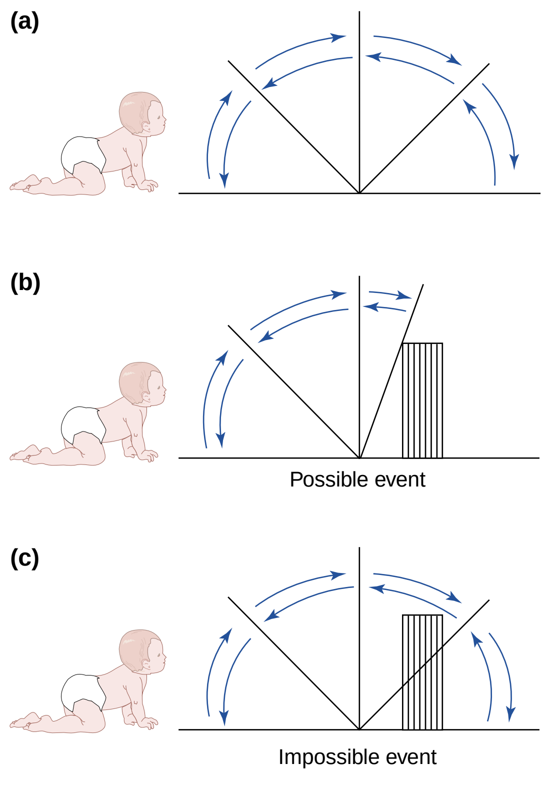

Fig. I. An experiment using the violation-of-expectation method to test infants' memory for hidden objects[c]. After infants viewed a drawbridge-like stimulus rotating back and forth (a), a block was placed in the path of the drawbridge. In the 'possible' event (b), the drawbridge rotated to the point where it would touch the block and then rotated back to its starting point. In the 'impossible' event (c), the drawbridge appeared to rotate through the space occupied by the block before rotating back to its starting point.

In one of the most well-known studies using this method[f], infants viewed a drawbridge-like stimulus rotating back and forth, and then saw possible and impossible events involving the drawbridge and a block that became occluded by the drawbridge (Fig. I). Infants as young as 3.5 months looked longer at the impossible event, indicating some apparent memory for the occluded block. The dissociation between the sensitivity of infants in such violation-of-expectation studies and their failure to search for hidden objects is one of the most salient in memory development.

Such dissociations are observed even within search tasks. For example, infants appear to reach for toys that are hidden by completely darkening a room[g,h] months earlier than they will reach for toys that are hidden by visible occluders in the light. From a graded representations approach, a weak memory of an occluded object might be strong enough to guide a reach in the dark, when there is no direct visual information conflicting with the memory of the object. This same memory, however, might not survive the interference from the visual stimulus of an occluder where the object used to be[i]. This graded representations account predicts that infants might search more for an object that has been hidden behind a visible occluder if the room lights are then turned off (reducing the interference from the occluder on the weak representation of the hidden object) compared with if the room lights are left on. Preliminary results from our laboratory support this prediction.

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nonetheless failing for several more months to search for desired objects that are presented and then hidden (see Box 1). A prevalent account of this dissociation is that the memory of young infants for hidden objects is intact, but separable systems for acting on this memory are underdeveloped (e.g. a problem-solving system for lifting an occluding cover to retrieve a toy underneath)[19–21]. Although problem-solving demands are likely to be part of the problem[22], they do not fully explain the dissociation. When problem-solving demands are equated for retrieving visible and hidden toys, infants successfully retrieve visible objects while showing little memory for hidden objects, demonstrating that their failures with hidden objects cannot be due solely to problem-solving deficits[23,24].

According to a graded representations account, the abilities of infants to represent hidden objects become stronger with development; dissociations in memory for hidden objects result because weak representations of hidden objects suffice for some tasks but not others[23]. For example, a weak representation of a hidden object might allow infants to recognize a strange event with that object in the violation-of-expectation paradigm. Such weak representations might not suffice for reaching for hidden objects, owing to the greater complexity and effort of reaching. However, search failures would not simply reflect deficits in the action system for reaching; strong representations of objects (e.g. for visible objects) might be sufficient to drive the reaching system. This graded representations account of dissociations in memory development parallels the account of dissociations in optic aphasia. In both cases, particularly poor performance arises when tasks tap the interaction between two pathways with weak representations (the naming of visually presented objects or reaching for hidden objects), with relatively spared performance when tasks tap only one pathway with weak representations (gesturing the use of a visually presented object, naming an auditorally presented object, recognizing an impossible event with an occluded object and reaching for a visible object). A neural network model has demonstrated how graded representations can support the dissociations observed in memory development[23]. The model also predicted that infants would search more for familiar toys than novel toys after they were hidden (because familiar toys support stronger representations), whereas infants typically showed novelty preferences with visible objects. Preliminary work supports this prediction (Y. Munakata, unpublished observations).

Graded representations in executive functioning

Adults with damage to prefrontal cortex, infants and children show dissociations in executive functioning, appearing to know things but failing to act appropriately on the basis of this knowledge. For example, adults with prefrontal damage and children can verbally report new rules they have learned for sorting cards (e.g. to sort according to the color of the objects on the cards), but incorrectly sort the cards according to previously learned rules (e.g. based upon the shape of the objects on the cards)[3,4]. Similarly, infants can look to a new location where they have watched a toy being hidden, but incorrectly reach back to an old location where the toy was previously hidden[26–28]. Such compelling dissociations have suggested that action systems might be selectively impaired or underdeveloped while separable knowledge systems are fully functioning[28,29].

In contrast, according to a graded representations account, prefrontal representations might be weak because of neurological insult or state of development; dissociations in executive functioning result because weak prefrontal representations suffice for some tasks but not others[25,30–32]. For example, stronger representations might be required to resolve conflict. Sorting a card (e.g. a red truck) according to a new rule requires resolving a conflict (e.g. between the new rule of color and the previous rule of shape). In contrast, answering a standard verbal question about the new rule (e.g. 'Where do red things go in the color game?') does not involve any conflict. This graded representations account predicted that the dissociation between sorting and verbal measures would disappear when the amount of conflict in the two tasks was equated (e.g. by adding conflict to the verbal query by asking, 'Where do red trucks go in the color game?'). This prediction has been confirmed in children[25]. Similarly, a weak prefrontal representation of a hidden object might allow infants to gaze correctly at the location where the object is hidden, whereas a stronger representation is needed to overcome the prepotent response to reach back to a previous hiding location. This graded representations account was instantiated in a neural network model that (like infants) gazed more frequently than it reached, allowing the gazing system to make better use of weak representations of hidden objects[32].

Graded representations in language

People with phonological dyslexia have difficulty reading non-words (e.g. 'nust'), despite being able to read regular words (e.g. 'mint') and exception words (e.g. 'pint'), and to repeat non-words after hearing them. Again, this dissociation leads to the assumption that phonological dyslexia cannot result from damage to a general phonological system; otherwise, people with phonological dyslexia would not be able to read words or repeat non-words after hearing them. One account of these dissociations thus posits two systems for transforming information from print (orthography) to sound (phonology): a word-specific system that is preserved in phonological dyslexia and a grapheme-to-phoneme conversion system that is impaired in phonological dyslexia[33].

By contrast, according to a graded representations account, the dissociations observed in phonological dyslexia result from the weakening of general phonological representations, and the effects of these weak representations on an interactive language system including orthography and semantics[5,34,35]. Specifically, weak phonological representations might suffice for people to respond appropriately given other (non-phonological) support, as is available for reading words (semantic support) and for repeating non-words after hearing them (auditory support). These weak phonological representations might not suffice without such other support, as in the case of reading non-words (no semantic or auditory support). This graded representations account predicted that people with phonological dyslexia would show decreasing abilities to repeat words and non-words as the semantic and auditory support for them decreased. This prediction has been confirmed[5]. Furthermore,

Box 2. Explaining dissociations in terms of separable systems

Dissociations in recognition memory (between measures of recollection and familiarity) might be best understood in terms of the operation of two separate systems (the hippocampus and cortex). Consider the case of meeting a new person, and then encountering her a month later and recognizing her. Recollection refers to the retrieval of specific information about her (such as where you were when you met her, what her name is, etc.) in this recognition process. Familiarity refers to the assessment that she is known ('I know I've seen her before!'), without the recollection of specific information.

Recollection, but not familiarity, is associated with hippocampal activity[a]. When people recognize words that they have studied, hippocampal activity increases if they report recollecting the words, but not if they report that they know that they have seen the words without recollecting them (i.e. based on familiarity). In fact, hippocampal activity is similarly low for such recognized, non-recollected words as for new (also non-recollected) words. Furthermore, hippocampal damage impairs recollection but not familiarity, even when difficulty across tasks is controlled[b].

Computational considerations have also supported the notion of distinct roles for the hippocampus and cortex in memory[c]. Recollecting particular episodes requires rapid learning with non-overlapping representations. For example, recollecting meeting that particular person requires learning from a single episode and keeping that memory distinct from memories of meeting other people. The anatomy and physiology of the hippocampus make it well suited for this task (e.g. with relatively sparse representations that minimize interference). In contrast, representing the underlying structure of the environment requires slow, interleaved learning using distributed, overlapping representations. For example, abstracting a general schema for meeting people (e.g. what kinds of conversation are appropriate, how closely people stand) requires slow learning over multiple episodes, collapsing across the differences of meeting individual people. The cortex appears to be well suited for this task, and can also support familiarity based recognition. Thus, a fundamental computational trade-off in memory suggests the need for two specialized systems that the hippocampus and cortex appear to satisfy.

Finally, recollection and familiarity are associated with distinct event-related potential components, with different timing and spatial topography[d]. A relatively early frontal FN400 component varies with the familiarity of words, whereas a relatively late parietal component varies with the recollection of specific words.

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neural network models have demonstrated how an interactive system of phonology, orthography and semantics can support typical language processing (without specialized systems for regular words, non-words and exception words), and how damage to the system can lead to the dissociations observed in different types of dyslexia[16,34,36–38].

Conclusions

Behavioral dissociations cut across the domains of perception, attention, memory, executive functioning and language. These dissociations might be most salient during development and following brain damage, but are also observed in typical, adult populations (see, for example, Refs 2,14,39,40).

The graded representations approach provides a unified framework for understanding behavioral dissociations. Behaviors are viewed in terms of an interactive system that is sensitive to the strength of representations, which can vary based on factors such as environmental support, state of development and brain damage. Neural network models instantiating graded representations have simulated a range of dissociations and led to numerous predictions that have been confirmed empirically. This approach has shown promise to advance theorizing about how developmental transitions occur, and to inform intervention and rehabilitation.

These notions surrounding the nature of our cognitive systems might seem intuitive, or even obvious; they have been part of the cognitive literature for some time[41] and have been emphasized in both neural network and dynamic systems approaches[42]. However, numerous theories ignore the potential role of graded representations, instead treating knowledge as all or nothing and attributing dissociations to deficits in separable systems. It can be difficult within this kind of framework to think about how developmental transitions occur[43] or how to intervene or rehabilitate. How could children go from nothing to all, and how can individuals improve if critical separable pathways are simply missing? Furthermore, theories within this framework can become unwieldy in the number of separate systems

Box 3. Explaining associations as well as dissociations

Theories that posit multiple separable pathways to explain dissociations in behavior might have more difficulty accounting for related associations than graded representations approaches. Consider the case of reading, specifically reading regular words, non-words and exception words.

These tasks might seem like natural candidates for separable specialized systems. Regular words and non-words can be read according to rules about orthography-to-phonology mappings: 'mint' is pronounced according to the same rules that govern the pronunciation of 'hint' and 'lint,' and 'nust' follows the same rules that govern 'must' and 'rust.' In contrast, exceptions such as 'pint' violate such rules. And, regular and exception words might be 'looked up', based on prior experience, whereas non-words cannot. Further, behavioral patterns during development and following brain damage suggest separate systems specialized for different reading tasks. People with phonological dyslexia can read words but have difficulty reading non-words, whereas people with surface dyslexia can read non-words but have difficulty reading exception words. Thus, some theories of word reading posit two separate systems: a rule-based system for mapping orthography to phonology (for reading regular words and non-words, impaired in phonological dyslexia) and a look-up table for lexical items (for exception and regular words, impaired in surface dyslexia)[a].

However, there are also associations, or similarities, across the tasks of reading regular words, exception words, and non-words[b]. Many exception words show some systematicity in the othography-to-phonology mapping (e.g. in 'pint,' the pronunciation of the 'p', 'n' and 't', and even the pronunciation of the 'i' as in 'pie' and 'mind'), despite not following the most typical rules of pronunciation (as in 'mint'). Such 'neighborhoods' of similar and discrepant pronunciations influence the reading of regular words, exception words and non-words in both typical and brain-damaged populations[c–f]. A single system for reading regular and exception words and non-words can naturally handle the similarities across these tasks, and (as described in the main text) can account for the dissociations taken to suggest the existence of separable systems. In contrast, theories that posit distinct systems to explain the dissociations require special adjustments to account for the associations observed across reading processes[a,g].

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that must be posited to explain the array of dissociations observed during development, after damage and in the intact mature system.

Finally, two important caveats to behavioral dissociations should be noted. First, although graded representations provide a powerful tool for understanding dissociations across a range of domains, in some cases separable systems might provide the best explanation (see Box 2). This article emphasizes the importance of considering the potential role of graded representations, because in numerous other cases this approach appears to provide the best explanation, despite being ignored by prevalent accounts. Second, although dissociations are compelling and reliable, behaviors do often group together. That is, performance on one measure of knowledge often correlates with performance on a different measure designed to tap the same knowledge. These associations might fall out more naturally from a graded representations approach with interactive systems than from a separable systems approach designed to address dissociations (see Box 3). Theoretical frameworks must accommodate both the associations and the dissociations observed in behavior.

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Questions for future research

- Are different causes and consequences associated with different instantiations of gradedness (e.g. firing rates of neurons, coherence of firing patterns)?
- In other dissociations, such as speech versus gesture[44], why might one behavior require stronger representations than another behavior?
- If a common mechanism (the strengthening of representations) supports the ability to carry out new behaviors rather than old behaviors across a range of tasks (e.g. reaching to a new hiding location for a toy rather than an old one, sorting cards according to a new rule rather than an old one), what accounts for the discrepancy in the age when children succeed at these different tasks (one year of age for the hiding task[26], four years of age for the cardsort task[4])?
- Could weak representations be strengthened by using them for tasks that demonstrate sensitivity?
- What are further implications for drawing parallels across developing, brain-damaged, and mature neurologically intact populations?

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