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The representation of response effector and response location in episodic memory for newly acquired actions: Evidence from retrieval-induced forgetting ☆

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ABSTRACT

Information retrieval can cause forgetting for related but non-retrieved information. Such *retrieval-induced forgetting* (RIF) has been previously found for semantically and episodically related information. The current study used RIF to examine whether response effector and location are encoded explicitly in action memory. Participants learned unique touchscreen responses to ten novel objects. Correct actions to each object involved left-hand or right-hand pushing of one of four possible object buttons. After learning, participants practiced two of the ten object-specific sequences. Unpracticed actions could share hand only, button only, both hand and button, or neither hand nor button, with the practiced actions. Subsequent testing showed significant RIF (in retrieval accuracy and speed measures) for actions that shared hand only, button only, or both hand and button with the practiced action. The results have implications for understanding the representations mediating episodic action memory, and for the potential of RIF as a tool for elucidating feature-based representations in this and other domains.

1. Introduction

Throughout our lives we learn to master new motor skills, from tying our shoelaces to learning to play the piano to learning to drive. In the early stages of skill learning we may rely on episodic memories of performing the task. The more we practice a skill, however, the less reliant we become on explicit memories. Instead multiple episodes may be replaced by procedural memory, allowing us to perform the action with little conscious awareness (e.g., Fitts, 1964). What is represented in these episodes and how can this be investigated?

One potentially useful method for inferring the microstructure of episodic memory representations uses interference effects from the retrieval-practice paradigm to deduce what information is represented (e.g., Anderson, Bjork, & Bjork, 1994). In the original retrieval practice paradigm targeting semantic memory, participants studied categories of related items (e.g., Fruit — apple, banana, orange, strawberry; Bird — blackbird, robin, pheasant, finch). Participants then performed retrieval practice on half of the items from half of the categories (e.g., Fruit — apple, Fruit — banana), producing three item types which differed in retrieval status: practiced items from the practiced category (Rp+ items; Fruit — apple, banana); unpracticed items from the practiced category (Rp− items; Fruit — orange, strawberry); and unpracticed items from the unpracticed category (Nrp items; the Bird category). Memory for all three item types was finally tested in a memory retrieval test. Typically, two findings occur. First, as one might expect, practiced items (Rp+) are facilitated in comparison to unpracticed items from the unpracticed categories (Nrp) — the *retrieval practice effect*. Second, and more surprisingly, unpracticed items from the practiced category (Rp−) are impaired in comparison to the Nrp items (i.e., Rp−<Nrp) despite both being unpracticed — the *retrieval-induced forgetting effect* or *RIF*. RIF can occur not only for semantically related information, such as word lists (e.g., Anderson & Spellman, 1995; Anderson et al., 1994), but also for episodically related information (e.g., Ciranni & Shimamura, 1999; Koutstaal, Schacter, Johnson, & Galluccio, 1999; Noreen & MacLeod, 2013; Sharman, 2011).

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1.1. Use of RIF to study the micro-structure of episodic action memory

If RIF affects memory for actions, then it can be exploited in order to examine what is encoded in episodic action memory and could contribute empirically to discovering potential mechanisms underlying RIF. For example RIF could potentially reveal whether *action features* such as the response location (e.g., specific phone button) and response effector (e.g., hand) are explicitly represented in action memory. While Sharman (2011) has demonstrated that RIF can affect episodic memory for actions, use of the technique to reveal what is encoded in action memory has not been undertaken. Sharman showed that when an action is performed with a familiar object (e.g., phone — lift), other actions associated with the same object (e.g., phone — press key) are susceptible to RIF. While this finding suggests that the object is part of the action representation, it does not address whether RIF might be sensitive to what is encoded in episodic action memory — particularly what action features might be mediating behaviour.

Little is currently known regarding the representation of action features in *episodic memory for actions*. Much of the research on episodic action memory has been focused on the 'enactment effect' (see Roediger & Zaromb, 2010 for a review) whereby there is superior memory for action phrases (such as 'pick-up the pen') when they are followed by enactment of the phrases (with real or imaginary objects) during study as opposed to verbal learning alone (e.g., Cohen, 1981; Engelkamp & Krunacker, 1980; Paris & Lindauer, 1976; Saltz & Donnerwerth-Nolan, 1981). It remains unclear whether action representations in episodic memory include information about response location, response effector, or both. For example, performing a simple action such as pressing key 'b' with the right-hand index finger involves at least two action features: the *response effector* (right hand or right index finger) and the *response location* (key 'b'). If one or both of these features are represented in episodic action memory, then actions that contain one or both of the features could potentially show RIF.

There is both theoretical and empirical support for the explicit encoding of response location in action memory, while the question of whether response effector is encoded has received mixed support. A large number of studies using the Simon task (e.g., Heister, Schröder-Heister, & Ehrenstein, 1990; Riggio, Gawryszewski, & Umiltà, 1986), object affordances (e.g., Phillips & Ward, 2002), imitation (e.g., Bekkering, Wohlschlager, & Gattis, 2000; Hamilton, Brindley, & Frith, 2007), visual habituation (e.g., Woodward, 1998), neurophysiological approaches (e.g., Alexander & Crutcher, 1990), and brain imaging methods (e.g., Grafton, Hazeltine, & Ivry, 1998; Hamilton & Grafton, 2006), have suggested that response location, but not response effector, mediates performance. Studies using motor sequence learning paradigms designed to examine implicit motor memory (e.g., Nissen & Büllemer, 1987), have similarly provided evidence that motor sequence learning is effector-independent (i.e., not sensitive to which hand learned the sequence), at least during the early stages of learning (e.g., Berner & Hoffmann, 2009a; Kovacs, Muhlbauer, & Shea, 2009; Park & Shea, 2003; Verwey & Clegg, 2005; Verwey & Wright, 2004). Findings from these studies suggest that response location (and the end goal of actions) is explicitly represented in episodic memory, but the response effector may not be (e.g., Deroost & Soetens, 2006; Keele & Curran, 1995; Willingham, Wells, Farrell, & Stemwedel, 2000; Witt & Willingham, 2006; see Abrahamse, Jiménez, Verwey, & Clegg, 2010 for review).

In contrast to negative conclusions regarding the representation of response effector in action memory, other empirical evidence has led to the conclusion that response effector can be explicitly encoded. Some object affordance investigations have shown that left- or right oriented objects such as a frying-pan, can automatically evoke responses from a compatible effector (e.g., Tucker & Ellis, 1998). Similarly, stimulus–response (e.g., Rieger, 2004) and response-effect (e.g., Hoffmann, Lenhard, Sebald, & Pfister, 2009) compatibility phenomena have been shown to pertain to both the response location and the response effector. Interestingly, one of the critical pre-requisites for effector-dependent representations to be detected appears to be extensive practice in responding and interacting with stimuli (e.g., skilled typing: Jordan, 1995; Rieger, 2004, 2007; implicit sequence learning: Berner & Hoffmann, 2009a; Verwey & Clegg, 2005; Verwey & Wright, 2004; implicit movement learning: Kovacs et al., 2009).

In sum, previous studies have shown that stimulus-related actions are primarily mediated by spatial representations of response locations, while response effector representations appear to influence behaviour mainly after substantial amounts of practice or experience interacting with a stimulus or object. The application of RIF could potentially contribute to our knowledge by helping to determine whether response effector is represented in episodic action memory — even at an early stage of learning.

The current study examined whether RIF occurs for location and effector action features in episodic action memory. Encouragingly, RIF has been used to reveal feature-based representations in the past (e.g., Anderson & Spellman, 1995; Anderson, Green, & McCulloch, 2000 for verbal material; and e.g., Ciranni & Shimamura, 1999 for visuo-spatial material). If newly acquired object-related actions are represented in a feature-based format where both the response location and effector are represented in episodic memory, then RIF might occur for actions that share either one or both features with the practiced action.

Novel, vertically symmetrical objects were used and participants learned to interact with each of them by pressing a specific object button with a specific hand (Fig. 1). The task examined explicit, as opposed to implicit, action memory. This was ensured by instructing participants to learn a set of simple actions to each of 10 novel objects, and subsequently asking them to re-produce those actions. Both the intentional learning instructions and the subsequent request to consciously access the learnt object–action sequence associations, violate the major criteria for implicit learning (see Abrahamse et al., 2010 for review). This allowed us to examine episodic, newly acquired, as opposed to well-practiced object–action associations and to disentangle the representations of response location (button) and response effector (hand), by ensuring that there were no pre-potent responses to any of the stimuli, which may have contaminated the results, neither at the level of the hand (e.g., a frying-pan oriented to the right might automatically evoke a right-hand response to right-handed participant) nor at the level of the response location (e.g., the handle of the frying-pan may automatically evoke a response to its location).

Participants learned unique touchscreen responses to ten novel objects (Fig. 1A and B). Correct actions to each object involved lifting either the left or the right hand from a response box, and using the same hand, pressing one of four possible action buttons on the object via a touchscreen. After learning, participants practiced two of the ten object-related action sequences. There were four types of unpracticed actions: those that shared neither hand nor button associated with the practiced action (Nrp baseline); those that shared hand only (Rp — hand) or button only (Rp — button) with the practiced action; and those that shared both hand and button (Rp — both) with the practiced action. Retrieval accuracy and execution speed for the action were measured for all ten objects.

Assuming that RIF is sensitive to episodic action memory representations, there are at least three potential outcomes. First, if the action memory makes explicit only the response location (object button) but *not the response effector* (hand), as suggested by the majority of evidence on action memory, then significant RIF would occur for unpracticed actions that share response location but not response effector with the practiced actions. Second, if episodic action memory makes explicit both the response location (button) and the response effector then significant RIF would be observed for unpracticed actions that share either of the two features with the practiced action. Third, if the response location and response effector are represented as a unitary episodic representation of the action sequence as whole, then there should be significant RIF for actions that share both hand and