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Beyond action observation: Neurobehavioral mechanisms of memory for visually perceived bodies and actions

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Abstract

Examining the processing of others' body-related information in the perceivers' brain (action observation) is a key topic in cognitive neuroscience. However, what happens beyond the perceptual stage, when the body is not within view and it is transformed into an associative form that can be stored, updated, and later recalled, remains poorly understood. Here we examine neurobehavioural evidence on the memory processing of visually perceived bodily stimuli (dynamic actions and images of bodies). The reviewed studies indicate that encoding and maintaining bodily stimuli in memory recruits the sensorimotor system. This process arises when bodily stimuli are either recalled through action recognition or reproduction. Interestingly, the memory capacity for these stimuli is rather limited: only 2 or 3 bodily stimuli can be simultaneously held in memory. Moreover, this process is disrupted by increasing concurrent bodily operations; i.e., moving one's body, seeing or memorising additional bodies. Overall, the evidence suggests that the neural circuitry allowing us to move and feel ourselves supports the encoding, retention, and memory recall of others' visually perceived bodies.

Keywords: Memory, Action observation, Action perception, Body perception, Body stimuli, Motor imagery, Mirror neurons, Working memory, Sensorimotor recruitment, Embodiment, Motor memory, Motor simulation

1. Introduction

Adaptive behaviour in our highly social environment involves observing, recognising, understanding, learning, and imitating others' bodily actions. Examining the processing of others' bodies in the perceiver at the neural and behavioural levels is one of the key topics in cognitive neuroscience. Searching terms related to 'body perception' in Google Scholar reveals a steady number of hits (4.708.600 in 2000–2009, ~5 million in 2010–2019). This interest is driven by the advent of novel research techniques and the examination of neurotypical and clinical populations (e.g., Williams et al., 2001; Rizzolatti et al., 2009; Bolis and Schilbach, 2018; Galvez-Pol et al., 2020). In the current review, we specifically focus on the processing of others' bodies beyond the perceptual stage: perceiving another person's body and transforming such percept into an associative form that can be stored, updated, and later recalled (e.g., a body-related memory used to recognise or imitate previously seen body movements). By examining the processing of body-related memories, we combine the research fields of memory and action observation. The result moves forward the current understanding in the memory processing of multifaceted stimuli (i.e., bodies), as well as the embodiment and action perception frameworks.

Many studies in the memory field, especially those examining working memory, have used non-body-related stimuli such as coloured squares, lines, sequences of numbers or letters, and shapes. As noted by D'Esposito and Postle (2015), two branches have developed within this literature: one studying and using symbolic stimuli that are usually considered to be semantic (e.g., words), and another branch whereby the target stimuli are considered to be perceptual (e.g., coloured shapes). In the latter case, the stimuli per se do not easily elicit a meaningful depiction of information; henceforth we refer to these stimuli as arbitrary stimuli. Despite differences, both branches do acknowledge the existence of non-overlapping memory systems to store different types of stimuli such as those based in semantic or visuospatial properties (Baddeley, 2012). Importantly, an additional memory system to store visually perceived static bodies and dynamic actions was originally proposed by Smyth and colleagues. These authors provided behavioural evidence of a system to encode, recall, and maintain observed actions in memory (Smyth et al., 1988; Smyth and Pendleton, 1989). Notably, these and other studies suggest that this memory system for body-related stimuli is partly underpinned by the neural circuitry allowing us to move and feel our body, that is, motor and somatosensory representations of the body in the brain. Accordingly, we first introduce others' body as a type of stimulus with unique features. Secondly, we briefly summarise some of the findings of the general memory field and situate these in memory studies involving body stimuli to-be-remembered. Thirdly, we review behavioural evidence of a memory system to store bodily stimuli –related to observed bodies and actions. Specifically, we review studies on memory for action recognition, action reproduction, and the memory capacity for these processes. Fourthly, we review the neural underpinnings of these cognitive processes. To this purpose, we consider three pieces of information: studies on action observation, sensory recruitment models (which propose resemblance between perceptual and memory mechanisms), and recent electrophysiological studies on action recognition. Last, most of the work revised here comes from studies on working memory. Yet, given the tight links between working memory and long-term memory (see Eriksson et al., 2015; Ngiam et al., 2019), it is likely that many of the results reviewed here expose overall memory mechanisms.

2. Behavioural evidence suggesting the presence of a memory system for body-related information

2.1. Introducing the body as a stimulus to-be-remembered

To better understand the memory processing of bodily stimuli, it is important to revise their use in the general memory framework. Most memory studies have not used bodily stimuli, but stimuli to-be-remembered that convey other types of symbolic information (e.g., words) or little to no symbolic information (arbitrary stimuli such as coloured lines). Bodily stimuli have intrinsic features that evoke associations beyond the stimuli per se, and they are more closely related to symbolic than to arbitrary stimuli. Here we use such a contrast to present a non-exhaustive list that characterizes the use and nature of bodily stimuli in the current memory literature:

Concerning the use of experimental paradigms, (1) in most memory studies participants have to detect differences between stimuli displayed in the first sample (i.e., memory phase) and the later test phase. However, in studies using images of body postures or dynamic actions, memory performance can be tested not only by asking participants to visually detect differences between the stimuli (i.e., action recognition; see Wood, 2007, 2009; Galvez-Pol et al., 2018a), but also by actively reproducing the body stimuli to-be-remembered with one’s body (i.e., action execution; see Smyth et al., 1988; Smyth and Pendleton, 1990). (2) The possibility of recalling bodily stimuli by reproducing the memoranda with one´s body highlights that a shared frame exists between the perceiver and the observed stimulus; i.e., the body. A common frame, between subject and stimulus, underpins the coupling between one’s body and others’ bodies. This coupling supports inferences about the use of our body by perceiving and interacting with others, which in turn seems to drive sensory signals about bodily percepts onto our body representation in the brain (Niedenthal, 2007; Rizzolatti and Sinigaglia, 2010; De Vignemont, 2011). (3) Particularly, the sight of a body does not only elicit recruitment of visual brain areas (Downing et al., 2001; Peelen and Downing, 2007), but also of somatosensory and motor brain regions (Keysers et al., 2004, 2010; Gazzola and Keysers, 2009; Caspers et al., 2010; Mukamel et al., 2010; Molenberghs et al., 2012; Hardwick et al., 2018). (4) The involvement of these brain regions is modulated by one’s bodily experience, as well as the degree of bodily elicitation encountered with the stimuli and task (Calvo-Merino et al., 2005, 2006; Jackson et al., 2005; Cross et al., 2006; Bruzzo et al., 2008; Arslanova et al., 2019).

(5) Similar to other symbolic stimuli such as words embedded in sentences, bodily stimuli depicting actions (vs. non-body arbitrary stimuli) are usually encountered in serial order with transitions

organised in a discrete, hierarchical, and goal-directed manner (Endress and Wood, 2011). For instance, one could memorize bodily stimuli that portray capricious intransitive actions or well-defined actions such as an arabesque in ballet (Smyth and Pendleton, 1989). Interestingly, memorising body forms such as patterned actions and fluent body movements seem to rely on different memory routes (Vicary and Stevens, 2014; Vicary et al., 2014).

Overall, the main difference between arbitrary and bodily stimuli is that participants can reproduce the latter by using their own body. Importantly, bodily stimuli can be encoded at different levels of abstraction and these usually correspond to those found within the action understanding framework (i.e., identification of the action, goal, and intention; Thompson et al., 2019). Lastly, it is important to notice that even non-body arbitrary stimuli can be recalled in an active manner (Wilken and Ma, 2004), possess different levels of complexity (Alvarez and Cavanagh, 2004; Luria et al., 2010), and intrinsic hierarchical properties (Brady and Alvarez, 2011; Xu et al., 2017). Nonetheless, bodily actions can be recalled by literally reproducing the memoranda; this degree of matching, between the subject (perceiver) and the encoded object, is difficult to meet with other types of stimuli.

2.2. Delineating memory systems using secondary/concurrent tasks

A well-known method to inspect if a cognitive system is dedicated to a specific process is by inserting an experimental manipulation that alters its regular functioning (Busiello et al., 2011). This can be accomplished by asking participants to perform a task (i.e., usually called secondary or suppression task) during the encoding, maintenance, and/ or recall of the stimuli to-be-remembered (i.e., primary memory task). The principle behind this approach is based on the limited capacity of any cognitive system. If a system is both limited in capacity and dedicated to a particular type of information (A but not B), it is possible to disrupt/overload its function by asking a participant to process additional A-related information. Conversely, adding B-related information should not interfere drastically with the corresponding cognitive processing. Initially, this approach aided to delineate visual, spatial, and verbal memory systems (as reviewed by Repovš and Baddeley, 2006). More recently, another memory system, for the encoding and maintenance of visually perceived bodily information, has been also conceptualised (Baddeley, 2012).

In this work, we have found a dozen behavioural studies that have specifically examined the memory processing of visually perceived bodily stimuli by using behavioural interferences. Importantly, bodies are multifaceted stimuli that can be encoded visually, verbally, spatially, motorically, etc. Therefore, researchers have aimed to dissociate the relevance of each one of these constituents by usually performing multiple experiments for each study. This enriches the conclusions that can be drawn from them. The subsequent experiments usually involve asking participants to observe, maintain, and reproduce or recognise actions. In addition, different secondary tasks that aim to interfere with the processing of specific types of information have been used. Because of the number of experiments within each study, we summarise the main findings in the below sections, as well as expand these by detailing each experiment in the Supplementary material, Table 1.

2.2.1. Memory for action reproduction

In memory studies of action reproduction, participants are usually asked to reproduce a number of actions after a brief delay. Hence, the experiments here belong to working memory studies. In some of these studies, participants are also asked to perform a motor, verbal, or spatial secondary task that aims to selectively disrupt the corresponding type of information processing. Importantly, even though the term motor secondary task is typically found in the literature, motor and sensory functions are coupled dynamically within a predictive framework (Wolpert et al., 1995; Kilner et al., 2007; Yon et al., 2018). Therefore, it is rather difficult to imagine a motor task with no sensory processing, henceforth in the current review, we use the term sensorimotor secondary task.

In the late eighties, Smyth et al. (1988) developed a new line of research studies in which they asked participants to memorise and then reproduce an increasing number of visually perceived actions (e.g., bending, crossing, straitening the limbs). During the observation of the actions to-be-remembered, the participants were also asked to either perform a sensorimotor, verbal, or spatial secondary task (body tapping, tapping locations in space, counting aloud). Across a series of experiments (see Supplementary material, Table 1), the authors showed that the number of correctly reproduced actions mostly decreased with the concomitant secondary sensorimotor task (i.e., body tapping), whereas the spatial secondary task did not significantly interfere with the memory span for actions and vice versa. The secondary verbal task also decreased memory span for actions, however, its effect seemed moderated by the familiarity of the participants with the actions to-be-remembered. In this regard, Moreau (2013) observed a similar effect when comparing novice and expert participants. (see further Expertise section). These results indicate that the extent to which verbal codes are used to memorize bodily stimuli varies according to the participants' experience with the stimuli.

Following the above study, Smyth and Pendleton (1990) showed that merely observing another person's body movements during the retention interval decreased the memory span of actions. In three different experiments the authors showed that after a short interval, the recall of bodily actions is affected by merely watching similar movements during the retention interval, also by reproducing similar movements, as well as by encoding another set of movements (additional memory load). Conversely, other types of secondary task that are not strictly related to bodily features, such as making or observing movements to spatial locations, did not interfere to the same extent with the memory span for bodily actions. Therefore, perception, action imitation, and additional memory load seem to impair one's capacity to transform visual information about other's bodies into representations that can be later retrieved from memory (schematic illustration in Fig. 1). Interestingly, the dissociation found by Smyth et al. (1988), and Smyth and Pendleton (1990) seemed rather independent of the laterality of the body part involved. Specifically, moving either the right or left hand during the observation of hand postures to-be-remembered reduces the memory span for such stimuli (Smyth and Pendleton, 1990). This is congruent with more recent studies that show bilateral activation of the hand area in the brain irrespectively of the stimulated hand (Rusconi et al., 2014; Tame and Longo, 2015; Tame et al., 2016, 2019).

The dissociative nature of the results found by Smyth et al. (1988, 1989), and Smyth and Pendleton (1990) was later replicated by Woodin and Heil (1996). These authors asked participants to remember bodily actions adapted from the above-mentioned studies or locations in space using the Brooks task (Brooks, 1967). In simultaneity to these memory tasks, participants were instructed to perform two secondary tasks aiming to disrupt visuospatial or bodily processing; i.e., a square tapping task and a body tapping task. The results showed that memory span for spatial locations decreased when accompanied by the square tapping task, whereas span for body configurations (number of correctly recalled actions) diminished when concomitant to the body tapping. Importantly, later studies also found a double dissociation between processing spatial and body-related information, even when the secondary tasks were controlled for difficulty. Rumiati and Tessari (2002) tested participants to remember actions related to the use of objects. In addition, they also performed verbal, sensorimotor, or spatial secondary tasks that were virtually identical in terms of cognitive demands. The authors found that the effect of the sensorimotor and spatial suppression could be dissociated even when they required a similar amount of cognitive resources. Interestingly, in another study, Tessari and Rumiati (2004) showed that encoding of meaningless and meaningful actions seems to rely on distinct memory processes. To reach this conclusion, they prompted participants to use different processing routes by manipulating the order and proportion of actions to-be-remembered. Their results showed that when trials of meaningless and meaningful actions are mixed in a block, participants seem to use that processing route allowing to store both types of actions.

2.2.2. Expertise in memory for actions

Numerous studies have compared the perceptual processing of naïve and motorically skilled participants such as dancers or athletes. This allows examining the effect of deep-rooted representations that are built through action execution on the processing of body-related information (Aglioti et al., 2008; Calvo-Merino et al., 2010). In the memory domain, it has been shown that compared to novice participants, skilled football players are better at recognising previously seen sections of a game (North et al., 2011). Similar advantage has been Found in experienced basketball players, who were better at recognising structured and unstructured sections of the games (Allard et al., 1980). Congruent with studies in other memory domains (Sala and Gobet, 2017), the effect of body expertise upon memory recall seems to span from structured to random domain-specific actions. Along the same lines, dancers' memory span is longer for both structured and unstructured dance movements (Starkes et al., 1987), and this advantage unfolds beyond their specific sensorimotor expertise; i.e., expert dancers seem to possess better encoding and lasting representations of dance and non-dance movements (Smyth and

Pendleton, 1994). This general superiority seems underpinned by a range of different encoding strategies such as the use of cues, the encoding of events as more or less meaningful, the verbalization of what is observed, or the use of imagery and synchronization (see compendium of encoding strategies in Starkes et al., 1990; Ille and Cadopi, 1999; Poon and Rodgers, 2000; Bläsing et al., 2012, 2018; Stevens, 2017; Stevens et al., 2019).

Regarding the effect of expertise, secondary tasks, and the memory processing of body movements, Cortese and Rossi-arnaud (2010) showed that a secondary sensorimotor task can reduce the number of correctly recalled movements in expert ballet dancers. Conversely, having to remember concurrent spatial locations only affected the correct recall of the locations on stage where the ballet movements had to be performed. In this line, Moreau (2013) also tested wrestlers and naïve participants to remember stimuli depicting arms or legs movements during either a verbal or sensorimotor secondary task. The results showed that naïve participants relied more on verbal codes than the wrestlers. Moreover, while the latter participants displayed an overall superiority of memory performance, the sensorimotor secondary task was more disruptive for the experts than for the naïve participants.

While the previous studies showed that the recall of bodily stimuli (e.g., actions) is impacted by adding bodily operations during the retention interval, there is evidence showing that also motor execution is affected by simultaneously having to memorise other actions. Respectively, Woodin and Heil (1996) asked participants to memorise spatial locations or actions similar to those in Smyth et al. (1988) while they were rowing. The on-going rowing involves two constant movements: body movements to spatially position the oar and ‘catch’ the water and the reposition of the body configuration to initiate the following catch (hands away movement). The results showed that encoding spatial locations impaired the participants’ catch but not the patterned hands away movement. Conversely, the encoding of body configurations interfered with the participant’s reposition of the body in the hands away movement, but not during the spatial catch with the oar. These results denote that memorising specific types of information and the execution of on-going actions might share some common mechanisms. The degree of this overlap seems to depend on the specific and dynamic nature of the concurrent tasks.

Overall, the above studies showed that remembering body-related stimuli seems to require similar computations than perceiving others’ bodies and moving one’s body. Contrariwise, having to remember other types of information (e.g., arbitrary stimuli, other non-body visual features, locations in space, etc.) did not disrupt to the same extent such a process. Only verbal processing has shown to modulate this effect, but this occurs according to the participants’ experience with the stimuli. This is congruent with the results of Frencham et al. (2003, 2004, 2006), who showed that successful mimicry of a sequence of hand gestures seems to partly rely on verbal strategies. Here it is important to note that in the study of Smyth and Pendleton (1989), participants had to remember sequences of hand gestures after a familiarisation phase. Therefore, novelty seems to summon specific strategies and resources, but with progressive bodily experience, participants seem to gradually move from verbal and conscious encoding to a more sensorimotor and implicit embodied encoding (see e.g., results of Gao et al., 2014).

2.2.3. Memory for action recognition

The previous studies showed that memory performance for bodily stimuli is diminished by concurrent tasks that prompt the use of one's body. Importantly, beyond the use of secondary sensorimotor tasks, Smyth and Pendleton (1990) also showed that memory for actions is disrupted by just observing other's actions during the retention interval. Moreover, other bodily computations such as holding a second set of actions or merely copying others' actions also decreased the memory span for body movements. These results indicate that even when body movements are used as a filler task, in the absence of memory demands, they can interfere with the recall of bodily stimuli to-be-remembered. Congruent findings have been reported during visual search and visual object tracking (Pylyshyn and Storm, 1988; Emrich et al., 2009). In these tasks, the perceiver actively represents information about the stimuli while also engaging in some other operations such as the filtering of distractors. As noted by Tsubomi et al. (2013), such operations may directly limit task performance or implicitly necessitate of the visual memory component. Analogously, the study of Smyth and Pendleton (1990) might indicate that sensorimotor processing is required for a variety of body-related tasks, including the perception, execution, and memory consolidation of actions.

Participants in action recognition studies have to detect differences between instances of actions and report these in the absence of action execution. In such a setting, Vannuscorps and Caramazza (2016) asked neurotypical individuals and individuals born without hands to remember configurations of hands or black and white visual patterns. The results showed that individuals born without hands had lower performance in the memory task using hand images, whereas performance was identical for the visual pattern task. This suggests that i) lacking imitative motoric processing might impede short-term memory for visually perceived actions and ii) that classical memory systems in the working memory literature (i.e., the phonological loop and visuospatial sketchpad) might not be utterly sufficient to encode bodily stimuli.

In other studies, participants do not only have to recognize differences between visual displays but also hold additional visual and spatial non-body-related information in memory. In this regard, Wood (2007) adapted a delay matching-to-sample paradigm from classical studies in working memory (e.g., Luck and Vogel, 1997; Vogel et al., 2005), showing that memorising arbitrary stimuli such as visual and spatial non-body-related stimuli did not interfere with the correct recall of actions (Wood, 2007, experiments 4–8). Across the seven experiments of Wood (2007), the number of correctly remembered actions was only disrupted by having to remember sequential information of either body or non-body-related stimuli. For instance, when images of bodies and objects were serially displayed and the task implied their simultaneous maintenance in memory (Smyth and Pendleton, 1990; Woodin and Heil, 1996; Wood, 2007; Vicary and Stevens, 2014; see Supplementary material, Table 1). These results suggest that mechanisms maintaining in memory bodily stimuli might support other types of non-body-related (Schubotz, 2007; Wood, 2007; Wurm and Schubotz, 2017). One hypothesis to be tested here is that regardless of the nature of the stimuli, the sequential presentation of stimuli might elicit apparent motion and that common computational resources are summoned for this process (see Shen et al., 2014, experiment 5).

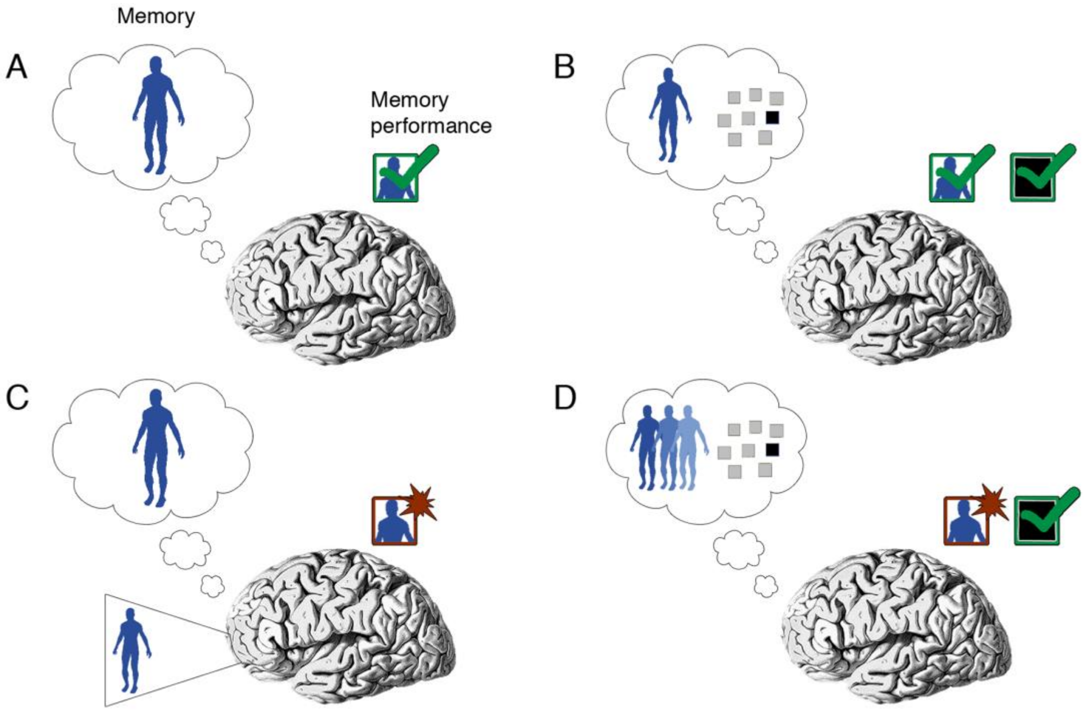

Fig. 1. Schematic illustration of body-related storage in a specialized memory system of limited capacity. A) Successful maintenance of a single body-related stimulus. B) Successful maintenance of a single body-related stimulus and spatial information in different memory systems; since the information does not belong to the same category, the stimuli are successfully maintained. C) Memorizing body-related stimuli while perceiving others' bodies (secondary task) results in exhaustion of common resources and poorer memory recall. D) Increasing the number of stimuli to-be-remembered (memory load) leads to poor performance during recall of body-related information. Conversely, this process does not disrupt the workings of memory systems specialized in other stimuli, leaving enough workspace for the correct recall of non-related bodily items (e.g., spatial).

2.2.4. Memory capacity and binding of body-related stimuli

While researchers are still investigating the exact mechanisms behind our working memory capacity (Ma et al., 2014; Constantinidis and Klingberg, 2016), there is general agreement on the limited capacity for the storage of information. Only between three and four simple visual stimuli can be simultaneously held in memory (Luck and Vogel, 1997). Others have found that even fewer items can be stored if these are more complex (Alvarez and Cavanagh, 2004; Brady et al., 2016). This capacity seems modulated, between other factors, by the participants' familiarity with the stimuli. Moreover, it can be indexed by using behavioural and neural measures of attention and memory capacity (Brady et al., 2016; Luria et al., 2016; Galvez-Pol et al., 2018a). Additional accounts also postulate than rather than memory capacity, familiarity modulates the precision of the percept in memory (Lorenc et al., 2014).

Regarding memory capacity for bodily stimuli, studies using the change detection paradigm have shown that only between two and three instances are well maintained in working memory (see converging evidence across Smyth and Pendleton, 1990; Wood, 2007, 2008, 2011; Shen et al., 2014; Ding et al., 2015; Gao et al., 2016; Supplementary material, Table 1). Yet, a greater number of properties, which are embedded in the stimuli, can be successfully stored in memory. For instance, nine bodily properties (e.g., type of action, duration of the action) distributed across three actions can be remembered as well as three properties across three actions (Wood, 2007). This suggests that binding bodily properties that are inherent to actions requires minor computational resources. On the contrary, having to remember actions and concurrent non-body-related features (e.g., agent or the background scenario of an action) seems to be a demanding process; as indicated by the low number of actions correctly remembered in these cases. Importantly, binding bodily and non-body-related visual features seems to decrease memory span in a monotonic manner, that is to say, irrespectively of the number of actions to-be-remembered (see Wood, 2008, 2010; Urgolites and Wood, 2013a, 2013b). Such a decrease implies that this binding does not engage the same system participating in the processing of bodily stimuli. Otherwise, an abrupt decay in performance would be likely observed.

Another way to examine memory capacity for bodily stimuli is by using points of light display depicting biological motion (i.e., using kinetic information from actions of a biological organism). In this regard, Shen et al. (2014) showed that memory capacity for biological motion is not affected by having to remember concurrent static non-body-related stimuli such as colours, locations, and shapes. Conversely, it diminishes by having to remember concurrent non-biological motion. Therefore, kinetic information, biological or not, might share a common memory storage. Concerning the binding of biological motion and non-body-related properties, it has been shown that only one or two action-colour bindings can be successfully maintained in working memory (Ding et al., 2015). Therefore, similar to previous studies using full displays of actions (Wood, 2008, 2011; Urgolites and Wood, 2013b), maintaining bound representations of biological motion and non-body-related information seems to be a demanding process. Ding et al. (2015) also examined whether distinct aspects of the binding (biological motion and colour) are involuntarily encoded when only attending to one of these features. Their results showed that: i) involuntary encoding did not take place, ii) and that maintaining this bound representation in memory did not require more resources than those needed to memorise the single features. Yet, it should be noted that these results contrast with the recent finding that an event-based encoding takes place for biological motions and spatial locations (see Gu et al., 2020).

Interestingly, further studies have linked working memory for biological motion and different facets of social information processing. For example, working memory capacity for biological motion, but not for arbitrary stimuli, predicts one's empathy (Gao et al., 2016) and theory of mind scores (He et al., 2019). Other work, using also biological motion, has shown that social actions are stored in working memory as chunks (Ding et al., 2017). Moreover, this process is nullified when the actions to-be-remembered are upside down (i.e., not in their canonical display). This later manipulation is congruent with the use of long-lasting representations during working memory (see Cowan, 2001; Eriksson et al., 2015; Ngiam et al., 2019) and the corresponding recognition of actions.

2.2.5. Wrapping up behavioural evidence of a memory system for bodily stimuli

The studies above suggest the presence of mechanisms, resources and system for encoding and maintaining visually perceived body stimuli in memory; these arise whether memory recall involves action recognition or action reproduction. The underpinning machinery is mostly disrupted by increasing the quantity of body-related information to-be-processed either in the visual domain or through the bodily engagement of the perceiver (e.g., moving one's body). Conversely, it is not disrupted by concurrent tasks involving non-body-related stimuli (e.g., colours, matrices, words) nor the binding of other visual features.

All in all, the compound of evidence suggests that: i) body and non-body-related stimuli are stored, at least partly, by using different systems. Moreover, the subsequent storage seems to recruit resources dedicated to move and feel one's body. ii) Alike visual working memory for arbitrary stimuli, where binding a conjunction of properties does not deplete memory capacity (e.g., binding colour and objects' length; Luck and Vogel, 1997), the binding of properties inherent to bodily stimuli requires small computational resources. Furthermore, these bound representations do not seem to require resources dedicated to the overall binding of information (see Liu et al., 2019).

iii) Along with the examined literature, we consistently found that memory for bodily stimuli is disrupted by increasing concurrent body-related load, for instance, when using secondary sensorimotor tasks. Yet, we also observed one more instance: it seems to be also disrupted by having to remember a concurrent sequence of non-body-related stimuli (Smyth and Pendleton, 1990; Woodin and Heil, 1996; Wood, 2007; Vicary and Stevens, 2014). A potential explanation for this effect is that a sequential depiction of stimuli can elicit apparent motion, which in turn might require processing resources that are also used to memorise dynamic actions. A more recent inspection of this matter by Shen et al. (2014) revealed that having to remember actions and arbitrary stimuli in motion do interfere with each other. Therefore, domain-general mechanisms devoted to the processing of motion are likely to be involved in the maintenance of bodily stimuli in memory.

3. Neural underpinnings of memory for body-related stimuli

Here we review neuroimaging and electrophysiological evidence of a system participating in the memory consolidation of bodily stimuli. Moreover, we contextualise these findings with the previously reviewed behavioural studies. To this aim, we first introduce the sensory recruitment models of working memory, which postulate the resemblance between neural mechanisms for perception and memory.

Secondly, we outline those brain regions participating in the observation and execution of actions. Lastly, we review neuroimaging and electrophysiological studies examining the memory recognition of bodily stimuli.

3.1. (Sensori)motor recruitment models: connecting dots between the memory field and neuroimaging data in action observation

A distributed network of brain areas supports the maintenance of stimuli in working memory (Postle, 2006; Christophel et al., 2017). Several studies indicate that part of the working memory storage is accomplished by allocating sustained attention to internal and sensory representations of the information (Awh and Jonides, 2001; Harrison and Tong, 2009; Carlisle et al., 2011; Gazzaley and Nobre, 2012; Kundu et al., 2013; Bettencourt and Xu, 2015). Instances of this process come from studies indicating that maintaining arbitrary stimuli in working memory such as coloured squares, auditory tones, and tactile taps elicit neural activity that is modulated by the number of stimuli to-be remembered in visual (Vogel and Machizawa, 2004; McCollough et al., 2007; Tsubomi et al., 2013), auditory (Huang et al., 2016), and somatosensory cortices (Harris et al., 2002; Katus et al., 2014), respectively. The sensory foundations of these activations and their modulation by memory load have led to postulate the sensory recruitment models of working memory (Pasternak and Greenlee, 2005; Postle, 2006; Harrison and Tong, 2009; Serences et al., 2009; Sreenivasan et al., 2014), also known as sensorimotor models due to the tight link between sensory attention and motor intention (D'Esposito and Postle, 2015).

These models and subsequent studies indicate that working memory is better characterized as a reestablishment of perceptual experience, in which transient maintenance of stimuli occurs in brain regions that also process the stimuli during perception and in the absence of memory demands (Tsubomi et al., 2013; D'Esposito and Postle, 2015; but see Xu, 2017). Moreover, this process seems to be modulated by long-term associations such as one´s experience with the stimuli, shaping the processing of these beyond early perceptual stages and extending the above findings beyond short-term based memory (McWeeny et al., 1987; Konkle and Brady, 2010; Brady et al., 2016; Ngiam et al., 2019). Crossing evidence that reports sensory recruitment in common memory tasks and sensorimotor involvement in action perception (resemblance amid perception and memory, and perception and action, respectively) allows examining past findings with new lenses: brain areas involved in action observation are likely candidates to maintain these stimuli in memory (Fig. 2). Henceforth, we outline these neuronal candidates.

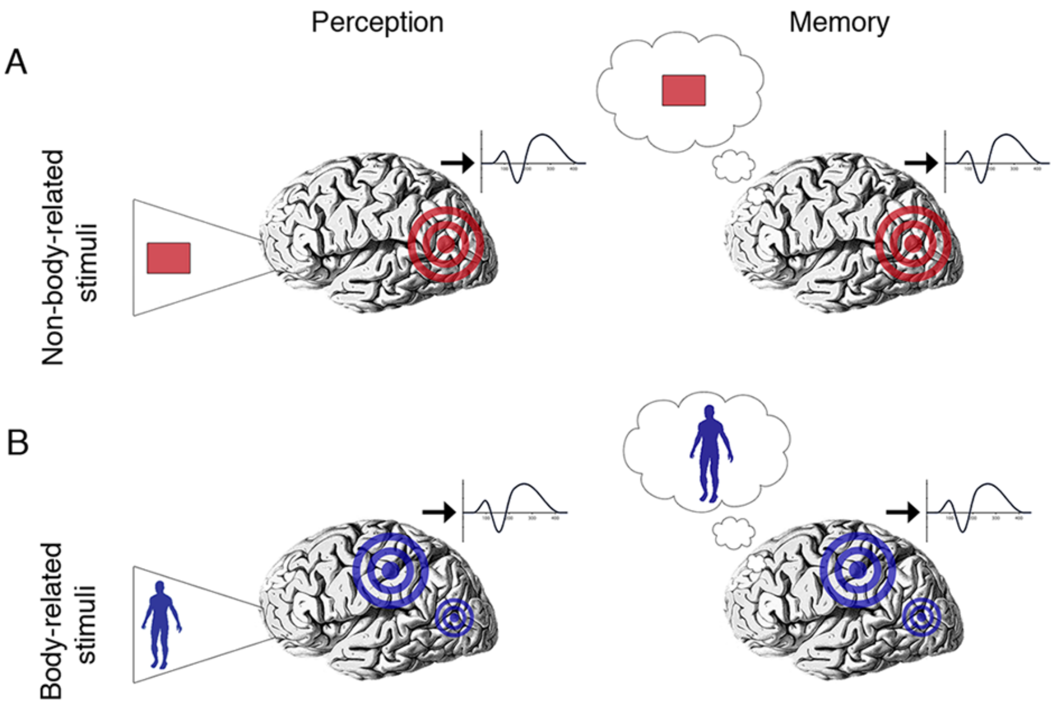

Fig. 2. Schematic illustration of sensorimotor and visual recruitment during memory maintenance of bodily and non-body-related stimuli. A) Visually perceiving stimuli such as coloured shapes elicits brain activity in posterior visual areas of the brain. Similar regions are recruited during the memory storage of the stimuli in memory (during the absence of online stimulus). B) Visually perceiving body-related stimuli elicits brain activity in posterior visual areas of the brain (the body is visually perceived), but also in more anterior frontoparietal brain areas; similar brain regions are recruited during memory storage/maintenance of the body percept in memory.

3.1.1. Brain regions participating in action observation are likely candidates to maintain bodily stimuli in memory

Neuroimaging studies have reported that different visual regions process the human body and its parts (fusiform and extrastriate body areas; Peelen and Downing, 2005, 2007; Urgesi et al., 2007a, 2007b). These regions hold strong connections with more anterior parietal-frontal brain areas, which are dedicated to the processing of body posture and actions (Zimmermann et al., 2018). In addition, the sight of bodily stimuli, including images of hands, whole bodies, and points of light display depicting biological motion, recruits a distributed complex known as the action observation network. The conceptualisation of this network develops from the original studies on the mirror neurons (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996) and includes the following brain areas across both hemispheres: ventral and dorsal premotor cortex, intraparietal sulcus (IPS) and intraparietal cortex, somatosensory cortex, superior parietal cortex, supplementary motor area (SMA), superior temporal sulcus (STS), the posterior middle temporal gyrus, the cerebellum, and visual regions related to body processing (Caspers et al., 2010; Rizzolatti and Sinigaglia, 2010; Molenberghs et al., 2012). These regions partially overlap and contribute to both the visual processing of others' actions and the execution of one's actions (Gallese et al., 1996; Sakai et al., 2002; Grèzes et al., 2003; Calvo Merino et al., 2005, 2006; Cross et al., 2006, 2009; Caspers et al., 2010; Kilner, 2011).

Studies on action perception have examined the influence of long-term memories in the perception of actions. These studies have shown that brain activity in different regions of the action observation network (e.g., premotor, parietal and inferior frontal brain areas, cerebellum) is modulated by one´s sensorimotor experience with the observed actions. Evidence for this comes from studies involving participants with various levels of sensorimotor expertise (e.g. expert dancers with particular acquired sensorimotor skill) observing actions within their motor repertoire (Calvo-Merino et al., 2005, 2006; Cross et al., 2006; Orgs et al., 2008). Importantly, the activity of these regions is further modulated by how the experience is attained. For instance, just by seeing actions and/or by actively learning them through motor practice (Calvo-Merino et al., 2006; Cross et al., 2006; Amoruso et al., 2014; Kirsch and Cross, 2015, see review from Turella et al., 2013). An interplay between visual and sensorimotor experience is observed in the form of reciprocal attenuations between parietal and more posterior cortices (Gardner et al., 2015); brain areas involved in processing images of bodies and visual input, respectively. These brain regions, typically associated with motor production and visual sensory processing, code action perception at different levels (Wurm and Lingnau, 2015). Inferior parietal and occipitotemporal lobes seem to code actions at more abstract levels, whereas the premotor cortex does it at more concrete levels (e.g., kinematics/ goals).

The tight links between perception, memory, and action, provide a point of reference to posit that sensorimotor brain regions participate in the maintenance of bodily stimuli in memory. First, behavioural studies have shown that maintenance of bodily stimuli in memory is disrupted by increasing the processing of body-related information. This effect was observed even when the additional processing did not explicitly demand an increase in memory load (i.e., just by observing an action or moving one's body; e.g., Smyth and Pendleton, 1990). Since then, neuroimaging studies have shown the involvement of sensorimotor brain areas during perception of actions, as well as the modulation of activity in these regions by long-lasting associations that are attained through diverse levels of sensorimotor expertise (e.g., Calvo-Merino et al., 2005, 2006; Kirsch and Cross, 2015; Hardwick et al., 2018). Interestingly, the off-line rehearsal of neural networks involved in action perception and action execution (i.e., premotor, parietal, and somatosensory cortices) partly overlap with those involved in motor simulation (Hardwick et al., 2018). This latter mechanism was well-defined long ago in the seminal work of Jeannerod (1994) with a striking resemblance to the aforesaid sensory recruitment models in memory. Specifically, it was defined as the mechanism allowing to activate our perceptual machinery in the absence of the original stimuli, as well as our motor system (and coupled sensorium) in the absence of executed actions (Jeannerod, 1994, 2006). More recent work supports the role of motor simulations in the formation of memories for bodily stimuli (Cook et al., 2014; Lu et al., 2016).

3.2. Neuroimaging studies on memory recognition of body stimuli

Beyond the crossing of memory studies with action observation studies, neuroimaging studies have directly examined the encoding and memory maintenance of bodily stimuli. The main aim of these studies is to inspect which brain areas show modulation of activity by memory load. Lu et al. (2016) examined the encoding and memory maintenance of increasing instances of biological motion (2 vs. 4). Their results showed that brain areas classically associated with the perception of biological motion and the action observation network were active. Specifically, an effect of memory load during the encoding was found in the middle frontal gyrus, parietal lobule, superior temporal sulcus, fusiform gyrus, and middle occipital gyrus. During memory maintenance, changes in activity were observed in the middle frontal gyrus, inferior frontal gyrus, and parietal lobule. Activity within the superior temporal sulcus was significantly modulated during the encoding but not throughout memory maintenance. As noted by Liu et al. (2019), the superior temporal sulcus seems to integrate information from the ventral and the dorsal pathways ('what' and 'where') into a coherent representation of biological motion (Saygin, 2007). However, the maintenance of biological motion seems to rely on the premotor cortex and the anterior area adjacent to the intraparietal sulcus.

More recently, Cai et al. (2018) showed that increasing the number of actions to-be-remembered (vs. objects, agents and locations; stimuli similar to Wood, 2007, 2008) modulates brain activity in the middle temporal cortex, which was shown to be functionally connected to anterior frontoparietal cortices. Cai et al. (2018) also observed that the superior parietal lobe was recruited during the maintenance of actions and locations in memory, and that specific patterns of brain activity emerged in frontoparietal regions depending on the type of stimulus. These results suggest partly similar neural processes for both types of stimuli, as well as the allocation of resources for memory retention from anterior to posterior regions (Curtis and D'Esposito, 2003; Stokes, 2015).

Altogether, the results of these neuroimaging studies indicate that the sensorimotor system supports the memory maintenance of bodily stimuli in memory. The recruitment of this system seems elicited by the nature of the information to-be-remembered. Moreover, not only bodily stimuli but also body-related stimuli seem to evoke activity within this system. Mecklinger et al. (2002, 2004) showed that memorising tools is associated with increased activity in the ventral premotor cortex of the dominant hand. Overall, the evidence reviewed in this section indicates that the sensorimotor system, via motor programs and motor simulations, underpins the retention of bodily stimuli in memory.

3.3. Electrophysiological studies on memory recognition of body stimuli

Other studies have used electroencephalography (EEG) to inspect how electric fields over the scalp change due to the encoding and memory consolidation of bodily stimuli. Using this technique, Gao et al. (2014) instructed participants to remember actions depicted by using biological motion with points of light display. The authors examined the effect of memory load upon a frequency band commonly taken as a neural index of sensorimotor processing (8−12 Hz; mu suppression). Across three different experiments, they showed that suppression of this frequency increased with memory load. However, this increase stopped when participants' memory could not hold more information in working memory (i.e., when reaching the limit of memory capacity). In a second experiment, Gao et al. (2014) prompted participants to use verbal codes during the encoding phase of the stimuli. They found that verbal encoding prevented sensorimotor engagement by abolishing mu suppression. These results expand the behavioural results of Wood (2007), as well as previous studies using concurrent secondary tasks (e.g., Smyth et al., 1988; Ding et al., 2015) by revealing the modulation of a neural signature classically associated to motor execution during memory retention (with no motor reproduction) of body stimuli to-be-remembered.

Beyond classical neuroimaging and frequency analysis techniques, new EEG methods that can capture the fast processing of body stimuli in the perceivers' brain have been developed. This is particularly relevant in EEG research because, despite its well-known properties (low cost, high temporal resolution, well-established paradigms), EEG possesses challenges that obscure data interpretation: signal propagation, its decay and cancellation, and the overall recording of superimposed activity from distinct neural sources. For instance, during the perception of bodily stimuli, the simultaneous activation of visual and sensorimotor brain areas makes difficult to dissociate the contributing role of these different regions. Considering this, Galvez-Pol et al. (2018a, 2018b, 2020) developed an EEG method that allows dissociating activity from visual, somatosensory, and motor cortices during the processing of body and non-body-related visual information; for full details see Galvez-Pol et al. (2020) and preceding work in Sel et al. (2014).

The method described above has been used to inspect modulations of brain activity by memory load in sensorimotor regions, beyond overlapping visual activity, during the consolidation of bodily vs. non-body-related stimuli. This has revealed that throughout the retention interval of the stimuli in memory, somatosensory and motor cortices exhibit changes in amplitude according to the number of bodily images to-be-remembered (Galvez-Pol et al., 2018a, 2018b). This modulation by memory load was not found for the control stimuli; i.e., polygonal shapes based on the outline, colour, and size of the bodily images. Moreover, Galvez-Pol et al. (2018a) and a more recent study using similar methodology and stimuli (Arslanova et al., 2019), have also shown that attending to bodily images involves modulation of somatosensory activity ~200−300ms after stimulus onset. The timing and modulation of brain activity in these tasks have been observed in other brain areas across classical paradigms of selective attention for non-body stimuli (e.g., in visual cortex; Eimer, 1996; Luck, 2012). Overall, these studies have isolated visually-driven neural activity in areas other than visual. By doing so, it has been possible to show that sensorimotor regions might play an important role in the encoding and memory consolidations of bodily stimuli over and above visual regions.

The finding that memory consolidation and attention modulate activity in sensory areas other than visual is not new. For instance, earlier work showed that attention influences activity in somatosensory cortices when searching or memorising tactile targets (Forster et al., 2016). While previous studies showed modulation of brain activity arising from areas congruent to the sensory modality of acquisition, the role of the content embedded in the percept remained unclear. The results of Galvez-Pol et al. (2018a, 2018b), Arslanova et al. (2019) and Sel et al. (2014) suggest that i) mechanisms involved in attention-based rehearsal do not only involve cortical regions originally used to perceive and acquire the information, ii) but that a more flexible mechanism operates according to the type of information embedded in the percept and task performed. As a consequence, when the perceivers' goal is to extract body-related information (e.g., memorise body posture), as opposed to non-body-related information such as colour, prior sensorimotor associations are recalled. This occurs even if the stimulus itself is the same, but attention is used to select different features (Fig. 3).

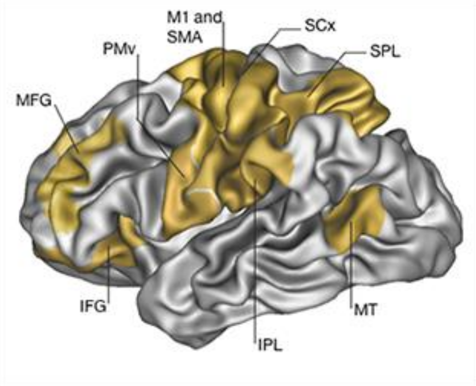

Fig. 3. Brain regions showing modulation of activity by memory load during maintenance of body-related stimuli in working memory. Highlighted areas are based on neuroimaging studies (Lu et al., 2016; Cai et al., 2018) and electroencephalogram studies dissociating or localizing neural generators (Galvez-Pol et al., 2018a, 2018b). All results are displayed on the left lateral-surface view. IFG, inferior frontal gyrus; MFG, medial frontal gyrus; PMv, ventral premotor cortex; M1, motor cortex; SMA, supplementary motor area; SCx, somatosensory cortex; IPL and SPL, inferior and superior parietal lobe; MT, middle temporal visual area. Mecklinger et al. (2002, 2004) showed neural involvement in PMv and IFG, but an increasing memory load was not used in their studies.

4. Conclusion

The present review concerns the encoding, maintenance, and recall of visually perceived bodily stimuli beyond the perceptual stage. To this aim, we first characterized the encoding of bodily stimuli as a particular type of memory process. This singularity is due to the presence of a shared frame (the body) between the perceiver and the stimulus; this supports the storage of associations that are built through bodily interactions. Secondly, we reviewed behavioural evidence suggesting the presence of a memory system for bodily stimuli. Specifically, we reviewed studies on memory for action recognition and action reproduction, outlined how these processes are modulated by expertise, as well as highlighted the capacity limits of the subsequent storage. These studies report that the sensorimotor system, between other roles, supports the memory storage of visually perceived bodily stimuli such as dynamic actions and static images of body postures. The reviewed evidence also indicates that given our limited memory capacity, 2 or 3 bodily stimuli are well maintained in working memory. Moreover, the correct recall of bodily stimuli is mostly disrupted by adding different forms of body-related processing. Conversely, this is not usually the case when other forms of processing are added. Last, we reviewed the neural underpinnings of these cognitive processes. To this aim, we considered studies on action observation, sensory recruitment models, neuroimaging and recent electrophysiological studies on action recognition. These studies support the idea that our sensorimotor system, the neural circuitry allowing us to move and feel our body, supports the encoding, retention, and recall of visually perceived bodily stimuli (e.g., actions). In this framework, it is worth noticing that while the current work covers the memory processing of bodily stimuli, there is compelling evidence showing that mnemonic traces of other types of stimuli/information also are dependent of the body (Casasanto and Dijkstra, 2010; Riva, 2018; Ianì, 2019). Memories do not unfold in a vacuum, but are at least partly, reenactments of the original bodily and somatic state, which are recalled via sensorimotor simulations.

Given the multifaceted nature of body-related stimuli, future work should address how different memory systems interact with each other; i.e., direct interactions vs. higher-level representations sustained by associational structures in the brain. To this aim, new work should aim to integrate the functional role of different brain regions in memory for visually perceived body stimuli. For instance, the cerebellum is known for its role in motor planning (Manto et al., 2012; Koziol et al., 2014) and the recognition of temporal and spatial relations among stimuli (Molinari et al., 1997). Yet, beyond traditional hand/arm motor tasks and action observation studies, no study has examined the modulation of cerebellar activity by memory load when memorising bodily stimuli. Further work should also examine how experience in one or more domains of the percept to-be-remembered (e.g., visual, motor, interoceptive) shape the corresponding interactions at the neural and behavioural levels. Lastly, well established findings in the overall memory study are still to be thoroughly examined. This includes the examination of the classical effects of stimulus presentation in memory consolidation (e.g., primacy, recency, length, and stimuli similarity; see Wood, 2007; Cortese and Rossi-Arnaud, 2010).

In conclusion, the reviewed research indicates that beyond action observation, our sensorimotor system supports the memory processing of visually perceived bodily stimuli. This process is certainly underpinned by daily interactions with the environment, including the reciprocity between one's body and others' bodies. These repeated perceptual stimulations are likely to be stored in the form of long-lasting associations by means of sensorimotor simulations (Jeannerod, 1994, 2006), which can be later used in ongoing tasks as enacted states of prior perceptual experience (i.e., much alike sensorimotor recruitment). Therefore, memorising bodily stimuli such as actions and body postures goes over and above the initial visual acquisition. Considering our moving cognition, it involves the neural machinery participating in the more functional and ecological processing of the stimuli to-be-remembered. On the whole, the evidence reviewed in the current work suggest that there is more to body images than meets the eye; we do not only remember others' bodies with 'our eyes in the brain', but also with our sensorimotor system and body-related regions in the brain.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.neubiorev.2020.06.014.

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Supplementary Material, Table 1 (*Beyond action observation: Neurobehavioral mechanisms of memory for visually perceived bodies and actions;* Galvez-Pol et al., 2020)

Behavioural studies using interference/secondary tasks to examine memory for bodily stimuli

Study	Exp	Task	Main experimental manipulations	Bodily stimuli to-be-remembered	Non-body stimuli to-be-remembered	Type of recall for bodily stimuli	Main findings
Smyth et al. (‘88)	1	Serial encoding of body movements and words (similar in *Exp. 1* and *2*)	Presence of articulatory suppression	Bending, crossing, and stretching limbs (*Similar actions in all experiments*)	Words	Action execution (*Similar in all Exp.*)	Articulatory suppression decreased recall of both body and non-body stimuli
	2		Presence of sensorimotor suppression		Words		Sensorimotor suppression decreased recall of body movements but not of words
	3	Serial encoding of body movements and spatial locations	Presence of sensorimotor or articulatory suppression		Spatial locations (Corsi Block task)		Articulatory and sensorimotor suppression, but not spatial, decreased recall for body movements. Sensorimotor suppression did not affect spatial recall.
	4	Serial encoding of familiar movements	Presence of sensorimotor or articulatory suppression		N.A		Familiarity decreases the effect of articulatory suppression.
	5	Serial encoding of familiar movements	Presence of spatial suppression		Spatial locations (Corsi Block task)		Recall of body movements did not affect spatial suppression, which impacted recall of spatial locations
Smyth & Pendleton (‘89)	1	Serial encoding of hand movements	Presence of sensorimotor or spatial suppression with left or right hand	Configurations of the right hand (finger positions / hand postures)	N.A	Action execution	Sensorimotor suppression performed with either the hand (left or right) decreased memory span for hand movements; absent effect of spatial suppression.
	2	Serial encoding of spatial locations	Presence of spatial suppression with left or right hand		Spatial locations (Corsi Block)	By pointing locations with right hand	Spatial suppression performed with either the hand (left or right) decreased memory span for locations movements.
							Further analyses: Exp. 1 and *2* showed that suppression tasks become slower when matched with alike type of information to-be-remembered
Smyth & Pendleton (‘90)	1	Serial encoding of body movements (similar from *Exp. 1* to *3)*	Recall after immediate, delayed, or filled delay with articulatory, sensorimotor, or spatial secondary task.	Bending, crossing, and stretching limbs (*Similar in all Exps;* alike Smyth et al., 1988)	N.A	Action execution	Copying other’s actions during retention of actions in WM disrupts memory for movements.

	2		Recall after filled delay: i) watching other's actions or ii) 1 vs. 2 sets of actions to-be-remembered		Spatial locations (Corsi Block task)	By pointing locations with right hand	Just observing other's actions decreases memory span for body movements / Holding a second set of body movements impairs memory processing / Spatial-filler task impacted in a lesser degree memory for body movements.
	3		As above but recall of body movements with no order (free recall)		As above	As above	Similar to *Exp .1* and 2: watching or having to recall additional movements affects memory span for actions. Average immediate-free recall: ~4 actions.
	4	Encoding locations in space	Immediate recall, delayed, or filled delay with observation of sensorimotor or spatial task.		Spatial locations (Corsi Block)	By pointing locations with right hand	Serial recall was affected by just watching the pointing of locations (during the filler task); absent effect from watching body movements
							Overall results: seeing or doing body movements during the memory retention of actions impacts memory performance (in free and serial recall). Less interference is found when secondary tasks tasks are verbal or spatial.
Quinn & Ralston ('86)	1	Encoding locations in space while executing movements (*Similar in all Exp.*)	In/compatible arm movements during encoding locations to-be-remembered	N.A	Spatial locations (Brooks task) (similar in all *Exp.*)	N.A	Incompatible movements affected memory for spatial locations.
	2		Same as above but manipulating degree of familiarity with the tasks	N.A		N.A	Regardless of familiarity and subsequent allocation of attention, incompatible movements affected memory for spatial locations
	3		In/compatible movements were performed passively (arm being moved) or actively	N.A		N.A	Performing both active and passive arm movements while encoding locations in space led to poorer recall of locations in space
Woodin & Heil ('96)	1	Serial encoding of body movements and spatial locations (~ *Similar in Exp. 1-2*)	Presence of square tapping or body tapping during encoding of stimuli to-be-remembered	Actions: bending, crossing, straighting limbs (adapt. from Smyth et al., 1988 and similar in *Exp. 1-2*)	Brooks task (in both Exp.)	Action execution (*Similar in all Exp.)*	Similar to Smyth et al. (1988, 1989). Double dissociation between type of suppression and memory: square tapping affected memory for locations and body tapping affecting memory span for body movements.
	2		Rowing while encoding stimuli to-be-remembered				Selective impairment in continuous rowing movement: 'catch water' timing affected by encoding locations and patterned body posture 'hands away' disrupted by encoding body movements.

Rumiati & Tessari (‘02)	1	Serial encoding of actions (*Similar in Exp. 1* to *3*)	Presence of sensorimotor suppression and degree of familiarity with actions to-be-remembered	Meaningful actions (related to objects use) and meaningless actions (modified pantomimes)	N.A (Similar for all *Exp.*)	Action execution (Similar in *Exp. 1-3*)	Memory span for meaningful actions is better than memory for meaningless actions
	2		Presence of articulatory suppression concomitant to sensorimotor suppression or spatial suppression	Same as above			Articulatory + sensorimotor suppression affects more memory span for actions than articulatory-only and articulatory + spatial suppression
	3		Articulatory, sensorimotor, or spatial suppression	Same as above			Sensorimotor suppression affects more memory span for actions than spatial suppression
	4	Encoding of object pantomimes	Presence of articulatory, sensorimotor and spatial suppression	Words related to object pantomimes			Similar word recalling after suppressions. Sensorimotor and spatial suppressions required similar resources (e.g., effects not due to distinct difficulties in suppression tasks)
Wood (‘07)	1	Serial encoding of actions in change detection paradigm (*Similar in Exp. 1-4*)	Only the increasing number of actions	Avatar displaying meaningless actions (similar in all *Experiments)*	NA (*Similar Exp 1-4*)	Action recognition; change detection paradigm (*Similar in all Exp.)*	Only ~2.5 actions are remembered. Limited WM capacity highly limited.
	2		Duration of encoding: 500ms *vs.* 750ms.				As above, ~2.5 actions remembered independently of encoding time
	3		Participants have to remember also the type and duration of actions				Similar memory capacity
	4		Participants asked to also remember type, duration, and laterality of actions				Integrated representations of actions: It is possible to remember 9 properties distributed across 3 actions, as well as 3 properties distributed across 3 actions.
	5	Serial encoding of actions and objects in change detection paradigm	Encoding up to 3 actions and up to 6 other non-body stimuli.		Coloured squares (Simultaneous display)		Equal memory for actions regardless number of non-body-related stimuli maintained in WM / Diff. systems of WM (for observed actions and objects)
	6	As above	As above, but participants only recalled one stimulus type at the end of the trial		As above		Similar results to *Exp. 5*
	7	Serial encoding of actions and spatial locations	As above but participants had to recall actions or spatial locations (0 to 6 locations)		Locations in a grid		Similar results to *Exp. 5* and *6* / Diff. systems seem to underpin WM for observed actions and spatial locations.
	8	Serial encoding of actions and objects	Similar to *Exp. 5* and *6*.		Coloured squares in serial order		Memory span for serial actions affected by concomitant encoding of serial non-body-related

							information. Some WM processes are shared when encoding serial information.
Wood (‘08)	1	Serial encoding of actions and agents in a change detection paradigm (*Similar in all Exp.*)	Participants asked to remember either actions or agents’ actions, or both (similar in all *Exp*).	Avatar displaying meaningless actions (similar in all *Exp.)*	Agents of actions: avatars with diff coloured clothing)	Action recognition in a change detection paradigm (*Similar in all Exp.)*	Maintaining both agents and actions in WM consumes resources associated with binding. Agents and actions seemed to be stored in different WM systems
	2				Agents displayed in non-overlapping spatial locations		In *either* or *binding* conditions, memory performance reflected performance of the WM system with lowest capacity /
	3				Agents were presented with a 50ms gap		Similar to *Exp.1* and *2*
	4				Agent differed in colour/type of clothing, gender, age, and facial features		Similar to *Exp.1* to *3* *Overall conclusions Exp 1* to *3:* binding actions and agents requires binding features from different memory stores. Visual cues aid this process
Cortese & Rossi-Artnaud (‘10)	1	Serial encoding of ballet movements	Presence of spatial suppression (finger tapping)	Ballet movements were listened and not visually presented.		Action execution (*Similar in all Exp.)*	Spatial suppression did not interfere with memory span for ballet movements (Approx. 3.6 movements regardless suppression)
	2	Serial encoding of ballet movements in specific spatial locations	Presence of spatial or sensorimotor suppression	As above	Concurrent to ballet movements, locations visually displayed	Ballet movements performed in specific locations on stage	Sensorimotor suppression increased errors on recalling ballet movements when these are coupled with spatial locations.
	3	Serial encoding of locations in space	Same as above	N.A	Locations in space (crosses across stage)	Walking to locations on stage	Only spatial suppression increased the number of errors when recalling spatial locations
	4	Serial encoding of ballet movements	Similarity between ballet movements (list of similar *vs.* list of dissimilar movements)	As *Exp. 1* and *2*	NA	Action execution	More errors when ballet movements to-be-remembered were more similar. Equivalent to memory studies using words, similarity plays a role in WM for patterned movements
Moreau (‘13)	1	Serial encoding of body postures	Expert and non-expert participants. Presence of verbal and sensorimotor suppression.	Full body stimuli displaying movement of arms and legs.	NA	Action recognition in a change detection paradigm (*Similar in all Exp.)*	Body experts did better during *non-suppression* and *verbal suppression* conditions. The latter affected more the non-experts. Conversely, sensorimotor suppression affected more the experts.
Vicary et al. (‘14)	1	Serial encoding of dance-like actions (similar in both *Exp*.)	Encoding dynamic actions or snapshots of these actions	Dance-like actions from Calvo-Merino et al. (2005)	NA	Action recognition in a change detection	Congruency effects between encoding and test form: Greater performance for dynamic movements

						paradigm (*Similar in all Exp.)*	when preceded by encoding of dynamic stimuli and *vice versa*.
	2		Encoding static or dynamic actions and presence of static or dynamic spatial suppression	As above	Spatial locations at once (static) or serial (dynamic)		Recognition of dynamic stimuli was impaired by dynamic but not static spatial suppression. No effect of suppressions was found when encoding static actions
Shen et al. ('14)	1	Encoding of biological motion	Increasing number of actions	Points of light displaying actions. 1 to 5 actions showed at once (similar in all *Exp*.)	NA	Action recognition in a change detection paradigm (*Similar in all Exp.)*	Only two to three actions can be retained. With longer encoding performance increased by one more action.
	2	Encoding of biological motion and colours	Encoding biological motion, non-biological motion, or both (Similar in *Exp* 2 to 5)		Coloured figures		Doing both memory tasks (for biological motion and coloured stimuli) does not affect memory performance. Independency of systems.
	3	Encoding of biological motion and spatial locations					Memory for biological motion and spatial locations did not mutually affect each other.
	4	Encoding of biological motion and shapes			Geometrical shapes		Memory for biological motion and shapes did not mutually affect each other.
	5	Encoding of biological and non-biological motion			Circled stimuli, rotating and moving		Memory for biological motion is affected by maintaining non-biological motion.
Ding et al., ('15)	1	Binding biological motion and colour	Increasing number of actions, one to five serially presented	Points of light display depicting actions (similar in all *Exp*.)	Colour of the points of light display	Action recognition in a change detection paradigm (*Similar in all Exp.)*	Working memory capacity for bindings between biological motion and colour is demanding, only one or two actions can be successfully stored.
	2		Increasing number of actions, one to five, simultaneously presented				As before, capacity for bindings between biological motion and colour is demanding, one or two actions successfully stored.
	3		Increasing number of actions, one to five, serially presented, and increasing presentation time (5 sec. per action).				Similar to Exp.1 and 2, but with a small increase in the mean number of stored actions; yet ~2 actions were successfully stored.
	4	Encoding biological motion and ignoring concurrent features (colour)	Increasing number of actions, two or five actions serially presented.		Changes in colour of point of light display to-be-ignored		Differences in the colour of the points of light display (irrelevant feature) were not encoded in (i.e., colour change was not involuntarily encoded)

	5	Encoding colour and ignoring concurrent features (biological motion)		Changes in points of light depicting biological motion to-be-ignored			Differences in actions depicted by the points of light display (irrelevant feature) were not encoded (i.e., action change was not involuntarily encoded)
	6	Encoding biological motion, colours, or binding biological motion and colours	Single or concurrent encoding of stimuli features while performing task to deplete binding resources				Binding both biological motion and colour doesn’t require more resources than encoding single feature. This might be due to ceiling difficulty in both single and concurrent encoding.
Liu et al., (‘19)	1	Encoding biological motion and colour-shape bindings (*Same in all Exp.)*	Fixed binding load and variable biological motion (1 to 3 instances).	Points of light depicting actions simultaneously (similar *Exp.* 1-3)	Coloured geometrical shapes (similar in all *Exp*.)	Action recognition in a change detection paradigm (*Similar in all Exp.)*	Increasing encoding of biological motion (1 to 3 instances) impacted the fixed encoding (3) of colour-shape binding.
	2		Same as above but lengthening the time to encode the stimuli to-be-remembered				Lengthening exposure made the above differences disappear. Increasing encoding of biological motion did not impact fixed encoding of colour-shape binding.
	3		Variable binding load (2 to 4 instances) and fixed biological motion (1)				Increasing number of bindings did not impact memory for biological motion. i.e., independent storage
	4		Fixed binding load and variable biological motion (0 to 3 instances).	Points of light depicting actions serially (similar *Exp.* 4-5)			Increasing encoding of biological motion did not disrupt fixed encoding of colour-shape binding.
	5		Variable binding load (0, 2, 3 or 4 instances) and fixed biological motion (3)				Increasing number of bindings did not impact memory performance for biological motion

Behavioural studies using interference/secondary tasks to examine memory for bodily stimuli. Overall, these studies reveal that memory processing of visually encoded body-related stimuli is selectively disrupted by adding concomitant tasks related to bodily computations; Study: authors and year of publication in parenthesis; Exp: experiment number in study; Main experimental manipulation: core task; body and non-body stimuli to-be-remembered: stimuli used for the primary and secondary task; type of recall: whether memory performance was tested via execution or recognition of the bodily memoranda; Main findings: key results in the framework of this review; WM: working memory; N.A: not applicable

Additional Reference; Table 1.

Quinn, J. G., & Ralston, G. E. (1986). Movement and attention in visual working memory. *The Quarterly Journal of Experimental Psychology Section A*, *38*(4), 689-703. https://doi.org/10.1080/14640748608401621