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Letter to the Editor

Impaired short-term memory for hand postures in individuals born without hands

Gilles Vannuscorps [a,b,*] and Alfonso Caramazza [a,b]

[a] Department of Psychology, Harvard University, Cambridge, MA, USA
[b] Center for Mind/Brain Sciences, Università degli Studi di Trento, Rovereto, Italy

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The psychological and neurobiological processes underlying short-term memory for words and objects have been the focus of very numerous studies and of detailed hypotheses (Baddeley, Eysenck, & Anderson, 2014; D'Esposito & Postle, 2015). In contrast, the mechanisms that support the temporary storage of information about other's actions and body postures in memory remain largely unknown. This study focused on a specific issue related to this question: does short-term memory for body postures rely, at least partly, on imitative motoric processes?

The role of imitative motoric processes in short-term memory for body movement and postures draws support from two main lines of evidence: neuroimaging studies show that our brain is inclined to covertly imitate others' body movements and postures (Wilson & Knoblich, 2005) and behavioral studies demonstrate that short-term memory for body postures and movements is disrupted by concurrent motor tasks such as finger tapping (Moreau, 2013; Smyth, Pearson, & Pendleton, 1988; Wilson & Emmorey, 1997; Wilson & Fox, 2007). However, neuroimaging studies do not settle whether motor involvement serves short-term memory or another purpose; and concurrent motor execution could interact with memory by activating more abstract, modality-independent action and/or spatial representations. There is evidence, for instance, that executing task-irrelevant motor sequences also disrupt visuospatial short-term memory for non-biological stimuli (reviewed in Postle, 2006). Thus, no existing study relates conclusively short-term memory for body postures and imitative motor processes.

This study aimed at filling this gap. We compared the performance of seven individuals born with absent or severely shortened upper limbs and no history of phantom limb sensations (IDs; 5 women; mean age = 40.28), and of 19 typically developed control participants (11 women; mean age = 50.64) in a task measuring visual short-term memory for hand postures and in a task measuring visual short-term memory for non-biological patterns. This provided a key test for the question under investigation. The IDs are neurologically intact individuals who have developed exceptional foot dexterity from early life and perform routinely many daily life activities in total autonomy (e.g., they write with a pen, type on a computer keyboard, drive cars, eat with a fork, and so on; see for instance, Vannuscorps, Andres, & Pillon, 2014). However, they have never executed upper limb movement and, thus, are not endowed with the motor representations that would allow them to covertly imitate hand postures. On this basis, we can predict that if imitative motoric processes contribute to short-term memory for body postures, then, the IDs should have a smaller memory span for hand postures than the control participants, everything else being equal. Participants had normal or corrected-to-normal vision and gave written informed consent prior to the study, which was approved by the Committee on the Use of Human Subjects,

* *Corresponding author*. Department of Psychology, Harvard University, Williams James Hall, 9th Floor, 33 Kirkland St., Cambridge, MA, 02138, USA.
E-mail address: gvannuscorps@fas.harvard.edu (G. Vannuscorps).
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Harvard University (Protocol: IRB14-2556) and the Ethic Committee for Experiments involving human subjects of the University of Trento (Protocol: 2014-032).

The order of the tasks was fixed so as to allow comparison between groups and participants unbiased by possible order effects. Participants first performed a Visual Pattern Test (VPT) – a traditional measure of visual short term memory (Della Sala, Gray, Baddeley, & Wilson, 1997). They were shown black and white checkered patterns of increasing size and complexity for 1 sec and, following a retention interval of 5 sec, were asked to recall the pattern by marking the squares in an empty grid of the same size. The task was terminated after three successive errors and the score was the maximum number of correctly filled cells in the most complex pattern recalled.

Participants then performed an action memory task. They were shown 64 series of two pictures, each depicting a left and a right hand in a given configuration (hands crossed or parallel), posture (palm or back view) and finger configuration (all or only the index finger stretched), and then asked to decide whether a third picture was the same as one of the two previously presented ones. The first two pictures were shown for 3 sec each with a 50 msec interval and the retention interval was 3 sec. Participants responded verbally (yes/no) and the responses were recorded online by the experimenter. Following the signal detection framework (Macmillan & Creelman, 2005), estimates of d-prime– a measure of signal detection sensitivity – were obtained for each participant on the basis of their hit and false alarm rates.

The results, shown in Fig. 1, are in line with the hypothesis that imitative motoric processes can support short term memory for body postures: (1) a mixed analysis of variance performed on the standardized scores of the participants in the two tasks with SUBJECT as the random factor, EXPERIMENT as within-subject factor and GROUP as between-subject factor showed a significant GROUP × EXPERIMENT interaction [$F(1, 24) = 8.91$, $p < .01$; $\eta p^2 = .27$]; and (2) post-hoc analyses showed that the IDs performed significantly below the controls in the action memory task [$t(24) = 3.13$, $p < .01$, $d = 1.42$] but not in the VPT [$t(24) = -.18$, $p > .85$, $d = .08$]. Additional analyses conducted to further clarify the results of the action memory task showed that, in comparison to the controls, the IDs had a lower hit rate [Controls' mean = 91.4%; IDs' mean = 87%; $t(24) > 1.67$, $p \leq .05$, $d = .74$], a larger false alarm rate [Controls' mean = 27.3%; IDs' mean = 41.9%; $t(24) > 1.67$, $p \leq .05$, $d = .95$] but a similar (liberal) response bias [Controls' mean $\beta = .67$; Ids' mean $\beta = .62$; $t(24) < 1$, $d = .21$; Macmillan & Creelman, 2005].

Thus, individuals born without upper limbs have difficulty in keeping pictures of hand postures in memory even for a short duration. If this effect were an artifact of experimental demand characteristics (Orne, 1962) or if it were due to task-related anxiety in the IDs at the thought of participating in an experiment involving the processing of hand postures, then the IDs would have been expected to have difficulties in any task involving the processing of hands or hand postures. However, previous evidence has consistently shown that the IDs process visually presented hand postures and movements as accurately, as rapidly, and with the same sensitivity and biases as typically developed participants (Vannuscorps, Andres, & Pillon, 2013; Vannuscorps & Caramazza, 2015, 2016a, 2016b). This pattern of results also argues against an interpretation of the observed memory difficulty in the IDs in terms of attentional or perceptual differences between the two groups. Thus, our finding provide evidence that imitative motoric processes (or the lack thereof) support (or impede) short term memory for body postures.

Classical short-term memory models comprise two systems: a phonological loop, holding verbal information and a visuo-spatial sketchpad, storing visual and spatial information (Baddeley & Hitch, 1974). Evidence that these two systems are typically involved when subjects maintain body posture and movement information in short-term memory is compelling (e.g., Moreau, 2013; Wood, 2011) and the present results are consistent with this hypothesis since the IDs, despite being deprived of the possibility to imitate the

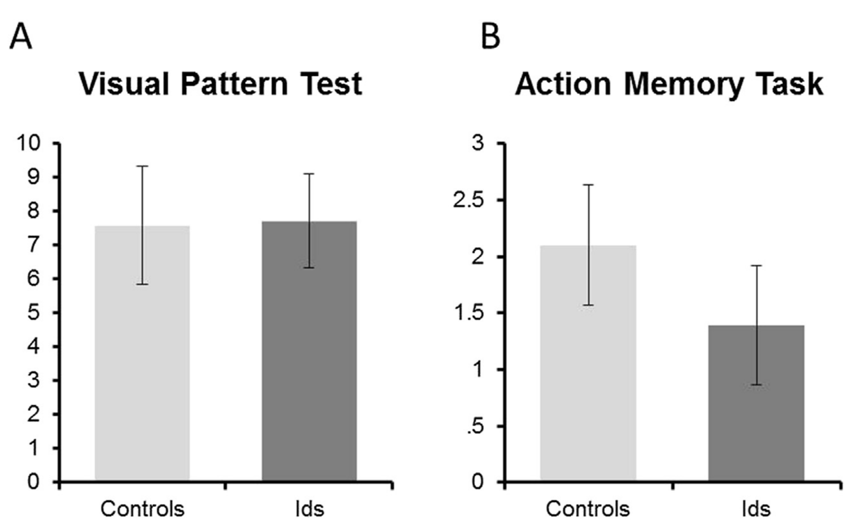

Fig. 1 – IDs' and control participants' maximum number of correctly filled cells in the most complex pattern recalled in the Visual Pattern Test (A) and d-prime sensitivity measure in the Action Memory Task (B). Error bars represent 1 SD from the mean.

observed hand postures, nonetheless performed the action memory task well above chance. Our findings, however, reveal that these two components alone are not sufficient to support fully efficient short term memory for human action information, and shed light on the existence of an additional, motor-related component of short-term memory devoted to the temporary storage and rehearsal of human action information.

In addition to this theoretical significance for models of short-term memory, this finding has also implications for the much debated question of the role of motor processes in human cognition. A highly influential hypothesis argued that imitative motoric processes are responsible for efficient perception, interpretation and/or prediction of observed actions (Rizzolatti & Sinigaglia, 2010; Wilson & Knoblich, 2005). Together with our previous finding that the IDs achieve typical efficiency in action perception and interpretation (Vannuscorps & Caramazza, 2015, 2016a, 2016b), this finding suggests instead that the primary contribution of imitative motor processes may be to maintain action information in short-term memory. Future studies should explore if and when short-term memory for action information contributes to perceptual tasks.

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