

ISSN: 0264-3294 (Print) 1464-0627 (Online) Journal homepage: <https://www.tandfonline.com/loi/pcgn20>

Conceptual processing of action verbs with and without motor representations

Gilles Vannuscorps & Alfonso Caramazza

To cite this article: Gilles Vannuscorps & Alfonso Caramazza (2020): Conceptual processing of action verbs with and without motor representations, Cognitive Neuropsychology

To link to this article: <https://doi.org/10.1080/02643294.2020.1732319>



Published online: 25 Feb 2020.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)



Conceptual processing of action verbs with and without motor representations

Gilles Vannuscorps^{a,b,c} and Alfonso Caramazza^{a,b}

^aDepartment of Psychology, Harvard University, Cambridge, MA, USA; ^bCenter for Mind/Brain Sciences (CIMEC), Università degli Studi di Trento, Rovereto, Italy; ^cInstitute of Psychological Sciences, Université catholique de Louvain, Louvain-la-Neuve, Belgium

ABSTRACT

Reading an action verb activates its corresponding motor representation in the reader's motor cortex, but whether this activation is relevant for comprehension remains unclear. To quantify the contribution of motor representations to the conceptual processing of action verbs, we measured the efficiency of two participants with atypical motor experience due to congenitally severely reduced upper limbs in processing verbs referring to actions that they had previously executed (e.g., writing) or not (e.g., shoveling) and compared the efficiency difference between the two verb categories to that found in typical participants, who had previously executed all these actions. This allowed measuring the contribution of motor representations unbiased by confounded low-level, lexical and semantic variables. Although the task was sensitive and the participants' performance was positively influenced by the richness of the words' conceptual representations, we found no detectable advantage for words associated with motor representations.

ARTICLE HISTORY

Received 30 August 2019
Revised 2 January 2020
Accepted 15 February 2020

KEYWORDS

Verbs; concepts; semantic knowledge; limb apraxia

Introduction

When a child learns to write, she slowly learns how to grasp the pen properly, how to coordinate her muscles, what strength must be applied, and so on. This learning is characterized, among other things, by changes in her motor system referred to as "motor representations". A hot topic of debate in current cognitive neurosciences concerns whether these motor representations play a causal role in the comprehension of action-related words (e.g., "to write").

A traditional view in semantic processing research is that motor representations do not contribute directly to the conceptual processing of action-related words. On this view, an action-related word is understood when perceptual and lexical processing of the word provides access to its associated conceptual knowledge (like the typical cause, purpose, the agent or instrument, the object of the action and so on), which is assumed to be represented separately from, and in a way that is qualitatively different than sensory and motor representations (Caramazza, Hillis, Rapp, & Romani, 1990; Landauer & Dumais, 1997; Tyler & Moss, 2001). This view does not imply that motor experience does not contribute to the acquisition of conceptual knowledge, but it assumes that

similar conceptual information (e.g., about the movements involved in an action) can be acquired through different modalities (e.g., action and vision).

In a departure from this view, recent proposals attribute to motor representations an important role on the conceptual processing of action-related words (Andres, Finocchiaro, Buiatti, & Piazza, 2015; Binder & Desai, 2011; Dreyer et al., 2015; Glenberg & Gallese, 2012; Kiefer & Pulvermüller, 2012; Pulvermüller & Fadiga, 2010). On this view, for instance, the loss of verb-related motor representations following damage to parts of the brain underpinning action execution is predicted to lead to selective difficulty to comprehend action-related verbs (Binder & Desai, 2011; Dreyer et al., 2015; Glenberg & Gallese, 2012; Kiefer & Pulvermüller, 2012; Pulvermüller & Fadiga, 2010). This position follows from the assumption, at the core of the embodied view of conceptual processing, that comprehending an action-related word is dependent on the reactivation of the motor representations acquired through motor experience with the corresponding action (Allport, 1985; Gallese & Lakoff, 2005; Pulvermüller, 1999, 2001, 2005).

To date, the evidence in support of these two competing hypotheses remains ambiguous. The

hypothesis that motor representations contribute causally to the conceptual processing of action-related words draws support from four main lines of empirical work: neuroimaging studies show that reading action-related words activates parts of the brain known to store motor representations (e.g., see for reviews, Fischer & Zwaan, 2008; Willems & Hagoort, 2007; but see also de Zubicaray, Arciuli, & McMahon, 2013; Watson, Cardillo, Ianni, & Chatterjee, 2013); behavioural studies demonstrate that people asked to execute movements do so more slowly or less smoothly when they read incompatible action-related words (e.g., Boulenger et al., 2006; Bub, Masson, & Cree, 2008); transient disruption of the (pre)motor cortex by transcranial magnetic stimulation (TMS) has been shown to affect the semantic processing of action words (Gerfo et al., 2008; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Willems, Labruna, D'Esposito, Ivry, & Casasanto, 2011) and many neuropsychological studies have reported associations between acquired action production difficulties and difficulties to name or comprehend action pictures (Albani, Pignatti, Mauro, & Semenza, 2010; Bak et al., 2006; Bak & Hodges, 2004; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bertella et al., 2002; Boulenger et al., 2008; Cotelli et al., 2006; Cotelli et al., 2007; Daniele et al., 2013; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Grossman et al., 2008; Grossman et al., 2008; Herrera & Cuetos, 2012; Herrera, Rodríguez-Ferreiro, & Cuetos, 2012; Hodges & Bak, 1997; Negri et al., 2007; Papeo, Negri, Zadini, & Rumiati, 2010; Péran et al., 2003; Pignatti, Ceriani, Bertella, Mori, & Semenza, 2006; Rodríguez-Ferreiro, Menéndez, Ribacoba, & Cuetos, 2009; Silveri et al., 2012; Silveri & Ciccarelli, 2007; Spatt, Bak, Bozeat, Patterson, & Hodges, 2002).

However, the neuroimaging and behavioural studies do not settle whether the activation of motor representations contributes to, or results from, the conceptual processing of action-related words (Mahon & Caramazza, 2008; Papeo et al., 2015; Wurm & Caramazza, 2019) and the interpretation of the findings from studies exploring the effect of TMS of the (pre)motor cortex on the conceptual processing of action-related word processing remains problematic in the light of the numerous contradictory results (e.g., Papeo, Pascual-Leone, & Caramazza, 2013; Papeo, Vallesi, Isaja, & Rumiati, 2009) and the fact that the neural effects of TMS are not limited to

the site of stimulation (Bestmann et al., 2008; Sandrini, Umiltà, & Rusconi, 2011). Likewise, the reported deficit for action-related words in patient with motor disorders is difficult to interpret because brain lesions in these patients also typically extends outside the motor system (Vannuscorps, Dricot, & Pillon, 2016).

In line with these limits, and in favour of the view that motor representations do not contribute to the conceptual processing of action-related words, there are reports of brain-damaged patients who achieve a normal level of performance in word/picture verification tasks, word/picture matching tasks, and in tasks that require the explicit retrieval of knowledge about actions despite extensive lesions in the motor system (e.g., Bartolo, Cubelli, Della Sala, Drei, & Marchetti, 2001; Negri et al., 2007; Rapcsak, Ochipka, Anderson, & Poizner, 1995). However, these studies measured only patients' accuracy in tasks with no time limit, leaving open the possibility that motor representations may nevertheless contribute to the speed or ease of conceptual processing without being indispensable (but see Vannuscorps et al., 2016).

Thus, additional work is needed to determine whether and if so to what extent accessing motor representations when reading or hearing an action-related word contributes to the semantic processing of that word. The most direct way to inform this issue is to compare the ease of conceptual processing of action verbs that are associated with motor representations to the ease of conceptual processing of action verbs that are not associated with motor representations, everything else being equal. If motor representations contribute to conceptual processing, then, there should be an advantage for the former in comparison to the latter proportional to the importance of motor representations to conceptual processing.

To test this prediction we recruited 20 typically developed participants (TPs) and two participants with atypical motor experience due to congenitally severely reduced upper limbs (Individuals with Dysmelia, IDs) and measured their accuracy and speed when asked to process action words referring to actions previously executed by all the TPs (i.e., associated with motor representations), but either previously (e.g., writing with the feet) or never (e.g., shoveling) executed by the IDs. The latter two categories of verbs are associated or not, respectively, with motor

representations in the IDs. We reasoned that if motor representations contribute to the conceptual processing of action-related words, then there should be a disproportionate efficiency difference between the two verb categories in the IDs in comparison to the TPs. This approach thus allowed measuring the contribution of motor representations in a within subject design unbiased by confounded low-level, lexical and semantic variables. Studying individuals born without upper limbs also protected us against the possibility that some actions that an individual has never executed may nevertheless be associated with some motor representations acquired through imitation learning (e.g., Buccino et al., 2004; Mattar & Gribble, 2005). This learning mechanism is assumed to rely on a parsing of the observed action into a series of effector-specific elementary movements (e.g., finger lifting, wrist turning) that are already part of the participants' motor repertoire, and on their recombination into a new motor sequence (Buccino et al., 2004; Byrne, 2003; Heyes & Foster, 2002). Individuals born without upper limbs being completely deprived of any upper limb representations, no motor representation could have emerged through observational learning of upper limb movement.

Participants' conceptual processing of action-related words was tested in a timed two-alternative forced choice concreteness judgment task. This task is particularly suited to address the role of motor representations in conceptual processing. First, it is the only task for which it has been unambiguously demonstrated that participants retrieve motor representations during the time period in which participants are accessing the meaning of the verb (Andres et al., 2015). In addition, this task has been shown to be particularly sensitive to the amount of knowledge associated with a given word and, therefore, appropriate to detect an effect of the availability of motor representations on the conceptual processing of action-related words (Pexman, Heard, Lloyd, & Yap, 2016; Pexman, Holyk, & Monfils, 2003).

Experimental study

Participants

We tested 2 individuals born without completely developed upper limbs (ID1 and ID2) and 20 right-handed typically developed control subjects (TPs).

ID1 is a 53-year-old man with a congenital bilateral upper limb dysmelia due to in-utero thalidomide exposure. ID1 had previously participated in several studies assessing the role of effector-specific motor simulation on action perception (Vannuscorps & Caramazza, 2016, 2017; Vannuscorps, Andres, & Pillon, 2013, 2014; Vannuscorps, Pillon, & Andres, 2012). In these studies, his typical efficiency in perceiving and interpreting observed hand actions motivated the conclusion that efficient perceptual processing of actions does not require effector-specific motor simulation (Vannuscorps et al., 2012; Vannuscorps et al., 2013, 2014; Vannuscorps & Caramazza, 2016, 2017). His congenital abnormalities include amelia of the left upper limb (i.e., the most severe form of dysmelia characterized by a complete absence of arm, forearm, hand and fingers) and, on the right side, a shortened right arm (± 12 cm humerus or ulna) directly fused to a hand composed of fingers 1 and 3 (shoulder, elbow and wrist joints absent or not functional). Given his lack of hand function ID1 developed exceptional foot dexterity from early life and routinely used his feet to achieve daily life activities (e.g., he writes with a pen, types on a computer keyboard, and eats with a fork). However, he reports being unable to use some familiar objects (e.g., a hammer or a saw).

ID2 is a 47-year-old woman with a congenital bilateral upper limb dysmelia of unknown origin. She did not take part in any of our previous studies. ID2's congenital abnormalities include shortened arms (± 30 cm) directly fused to the hands (no forearm, elbow or wrist) and oligodactyly of the hands (right hand: digits 1, 3 and a shortened thumb with two hypoplastic phalanges; left side: digits 1, 4 and a ± 1 cm rudimentary thumb with two hypoplastic phalangeal-like bones). The shoulder joints are anatomically and functionally typical. Therefore, ID2 can move her upper limbs in all directions by the normal range of movement allowed by the shoulder joint. ID2 achieves numerous everyday life activities with her stumps (e.g., driving her car) but she is nevertheless unable to use familiar objects (e.g., a needle or a shovel).

Among the 20 control participants, 9 were matched with ID1 (the ID1-Cs) for gender, age (mean = 53.55; range = 48–59; Crawford and Howell's (1998) modified *t*-test, $t(8) = -0.1$), and number of years of education (mean = 16.88; range = 14–19; modified *t*-test, $t(8) = 0.4$), and 11 (the ID2-Cs) were matched with ID2 for gender, age (mean = 48.54; range = 42–

52; modified t -test, $t(10) = -0.4$), and number of years of education (mean = 14.36; range = 12–19; modified t -test, $t(10) = -0.16$).

No participant had a history of psychiatric or neurological disorder or (in the case of the IDs) phantom limb sensations or movements. All had normal or corrected-to-normal vision.

Material and procedure

The initial set of stimuli was composed of 539 French verbs for which information regarding written name frequency were available in French lexical databases. In order to categorize these verbs along the concrete/abstract dimension, we presented these 539 verbs to 2 groups of 20 participants who did not participate in the main study (Group1: 14 women, mean age of 21; Group2: 16 woman, mean age of 20) and we asked them to judge on a five-point scale whether the verbs refer to actions involving movements of the upper limbs (1 = no movement; 5 = a lot of movement); we also asked them to judge how easily the verb arouses a mental image of the action to which it refers (1 = very difficult; 5 = very easy). The verbs with a rating equal or larger than 4 on both scales were considered as “concrete verbs” ($N = 177$) and the verbs with a rating equal or smaller than 2 on both scales were considered “abstract verbs” ($N = 121$).

In the main experiment, participants were seated in front of a computer screen located at a distance of about 60 cm and performed a block of 10 practice trials followed by five blocks of 50 trials and a sixth block of 48 trials. In each block, concrete and abstract words were mixed in a pseudo-randomized order identical for all the participants.

Each trial began with the presentation of a fixation screen depicting two horizontal lines positioned above and below a gap where a word would appear. Participants were asked to focus on the gap between the lines. After 2,000 ms, the stimulus verb was presented in the centre of the gap, in the infinitive form and in lower case (Courier New, 18); the horizontal lines remained on the screen. Individual stimuli remained on the screen for a duration of 2,000 msec or until a response was provided.

Participants were asked to decide as fast as possible whether the verb referred to a concrete or an abstract action. The following instructions were given to the participants in French:

“We ask you to decide as fast and as accurately as possible whether each verb presented on the screen refers to a concrete or an abstract action. Concrete actions refer to actions that involve body movements and that you can perceive if someone is performing it, such as ‘running’ or ‘eating’ or ‘yawning’. An abstract action refers to an action that does not necessarily involve any particular body movement and, therefore, cannot be perceived if someone else is performing it such as ‘thinking’, ‘hating’ or ‘hoping.’” (*“Nous vous demandons de décider aussi rapidement que possible et en faisant le moins d’erreurs possible si chacun des verbes présentés à l’écran réfère à une action concrète ou abstraite. Les actions concrètes sont des actions qui impliquent des mouvements du corps et que vous pouvez voir d’autres personnes réaliser, telles que ‘courir’ ou ‘manger’ ou ‘bailler’. Une action abstraite est une action qui n’implique pas nécessairement de mouvement du corps et, donc, que l’on peut ne pas voir lorsque d’autres personnes les réalisent, telles que ‘penser’, ‘haïr’, ou ‘espérer’.”*).

Then, the dysplastic participants were asked to respond verbally to the following instructions: “If the verb refers to a concrete action, then, say ‘concrete’ as fast as possible and if it refers to an abstract action, say ‘abstract’ as fast as possible.” (*“Si le verbe réfère à une action concrète, dites « concrète » le plus rapidement possible et si il réfère à une action abstraite, dites « abstraite » le plus rapidement possible”*). The controls were instructed to respond by key presses: “If the verb refers to a concrete action, then, press on the ‘C’ with your index finger as fast as possible and if it refers to an abstract action press on the ‘A’ with your middle finger as fast as possible.” (*“Si le verbe réfère à une action concrète, appuyez sur la touche « C » avec votre index le plus rapidement possible et si il réfère à une action abstraite appuyez sur la touche « A » le plus rapidement possible”*). “C” and “A” were written on, respectively, the keys “K” and “L” of an AZERTY laptop keyboard.

Note that in a verb concreteness judgment task, responding with an effector (e.g., the hand) typically involved in a concrete action (e.g., a manual action) provides a speed advantage (Andres et al., 2015). Thus, the use of verbal responses in the IDs and of manual responses in the controls in this study is likely to provide a speed advantage to control participants when responding to hand actions. This would be problematic when making a direct comparison between the performance of the IDs and control participants. However, the use of different response modalities in our study is not problematic because the objective here is not a direct comparison of the

efficiency of the IDs to that of the control participants. The theoretically relevant contrast in this study is the difference in performance for two types of hand actions across the two groups—any putative response advantage in responding manually to concrete action verbs for control participants is orthogonal to the contrast of interest here—an interaction of group by type of hand action.

The experiment was controlled by E-Prime software (Psychological Software, 2002, Pittsburgh, PA). The dysplastic participants responded by speaking into a sensitive built-in microphone connected with an RT-measuring PST (Psychology Software Tool) serial response box. They also performed a simple reaction time task before the experiment to familiarize them with the use of the microphone (avoiding any sound before the response, speaking loudly) and to verify/adapt the sensitivity of the microphone to the participants' voice.

Once the categorization task was completed, all participants were presented again with all the concrete verbs and asked to tell, for each of them, whether they had performed that action. From the 177 concrete verbs, only those that had been previously performed by all the controls participants of each groups were included in the analyses ($N = 156$ for the control group of ID1; $N = 158$ for the control group of ID2). These stimuli were then divided in two sets according to whether they refer to actions that ID1 and ID2 had each performed (verbs with motor representations, MR) or never performed (verbs with no motor representation, No-MR). The number and characteristics of the items in each set is provided in Table 1. Stimuli in Set 1 and Set 2 did not differ significantly in terms of spoken word frequency, imageability, and upper limb movements.

Analyses and results

The data that support the findings of this study are openly available (Vannuscorps, 2019). Trials with voice key failures (2 trials in ID1 and 7 trials in ID2) were discarded from all analyses. Categorization errors and trials in which no response was given before the trial timed out (i.e., after 2,000 ms; 1 trial in ID1, no trial in ID2, 8 trials in ID1-Cs and 15 trials in ID2-Cs) were scored as errors. There were no trials with very short response latency (<250 msec). No other trimming of the data was applied. Response

Table 1. Distribution of the stimuli in the various sets of items used in the categorization task (Abstract = Abstract verbs; MR actions = already performed concrete actions; No-MR actions = never performed concrete actions) and mean (and standard deviation) values of lexical and conceptual variables.

	Abstract	MR actions	No-MR actions	MR vs No-MR
ID1				
Nb of verbs	121	116	40	
Nb of letters	8.86 (1.82)	7.57 (1.66)	7.1 (1.5)	$p > 0.10$
Word frequency ¹	11.09 (27.6)	8.25 (33.84)	1.31 (2.06)	$p > 0.19$
Imageability ²	1.37 (0.43)	4.72 (0.25)	4.54 (0.26)	$p < 0.01$
Upper limb movements ³	1.3 (0.34)	4.81 (0.12)	4.83 (0.13)	$p > 0.43$
ID2				
Nb of verbs	121	130	28	
Nb of letters	8.86 (1.82)	7.66 (1.74)	6.89 (1.26)	$p = 0.03$
Word frequency ^a	11.09 (27.6)	7.39 (31.92)	2.29 (3.4)	$p > 0.40$
Imageability ^b	1.37 (0.29)	4.69 (0.26)	4.58 (0.23)	$p = 0.04$
Upper limb movements ^c	1.27 (0.11)	4.82 (0.12)	4.82 (0.13)	$p > 0.99$

^aNumber of lemma occurrences per million (New, Brysbaert, Veronis, & Pallier, 2007).

^{b,c}See Material and procedure section.

latency analyses were carried out over correct responses only.

We first conducted analyses to check the quality of the data and ensure that the task was sensitive enough to reveal typical effects of low level, lexical, and semantic variables on participants' response latencies. To this end, we performed linear regression analyses to examine the joint effects of the words' number of letters (New, 2006), frequency (log transformed lemma frequency; Howes & Solomon, 1951), and imageability (Balota, Ferraro, & Connor, 1991; Cortese & Fugett, 2004; Yap, Lim, & Pexman, 2015) as predictors of the IDs' and their controls' response latencies. The results of these analyses showed a significant joint effect of the three variables in predicting the response latencies of ID1 [Number of letters: Beta = 0.14, $t(255) = 2.27$, $p < 0.05$; Frequency: Beta = -0.13, $t(255) = -2.28$, $p < .05$; Imageability: Beta = -0.27, $t(255) = -4.28$, $p < .001$; Model: $R^2 = 0.15$, $F(3, 255) = 15.06$, $p < .001$] and his controls [Number of letters: Beta = 0.19, $t(272) = 3.12$, $p < 0.01$; Frequency: Beta = -0.16, $t(272) = -2.73$, $p < .01$; Imageability: Beta = -0.15, $t(272) = -2.6$, $p < .05$; Model: $R^2 = 0.12$, $F(3, 272) = 11.6$, $p < .001$]. The results also showed a significant effect of imageability in predicting the response latencies of ID2 [Number of letters: Beta = 0.05, $t(263) = 0.73$; Frequency: Beta = 0.03, $t(263) = 0.45$; Imageability: Beta = -0.25, $t(263) = -4.04$, $p < .001$; Model: $R^2 = 0.07$, $F(3, 263) = 7.07$, $p < .001$] and a significant effect of frequency and imageability in predicting

the response latencies of her control participants [Number of letters: Beta < 0.01, $t(273) = 0.1$; Frequency: Beta = -0.15 , $t(273) = -2.75$, $p < .01$; Imageability: Beta = -0.4 , $t(272) = -6.9$, $p < .001$; Model: $R^2 = 0.19$, $F(3, 273) = 21$, $p < .001$]. The outcomes of these analyses thus provide confidence in the quality of the data and in the sensitivity of the task. In particular, the finding that words' imageability was a significant predictor of response latencies in all groups demonstrates that our task was sensitive enough for the words' conceptual richness to influence participants' performance (Plaut & Shallice, 1993; Yap et al., 2015).

We then turned to our main question and tested the prediction that, if motor representations contribute to conceptual processing, then the verbs that are not associated with motor representations in the IDs (NoMR verbs) should be processed less efficiently in this task than the verbs associated with motor representations (MR verbs), everything else being equal (i.e., in comparison to the baseline provided by the controls' performance). To do so, we first computed an efficiency score (expressed in ms) for each participant and verb category by dividing the participant's mean response latency for correct responses by his/

her proportion of correct responses in each VERB CATEGORY (thus, the higher the score the poorer the performance). This score allows combining the measures of accuracy and speed into a single measure of processing efficiency and, thereby, between-group comparisons unbiased by potential speed-accuracy tradeoffs (Townsend & Ashby, 1978, 1983). Figure 1 displays ID1's, ID2's and their respective control participants' efficiency score for the two categories of concrete verbs in ascending order as a function of the size of the relative efficiency advantage for the set of action verbs associated with motor representations (MR verbs). From this Figure, it appears clearly that there was no disproportionately large advantage for the MR verbs in the IDs in comparison to the controls. ID1 and ID2 had a smaller advantage for the MR verbs than 5/9 and 5/11 of their controls, respectively.

To characterize these results statistically, we tested the differences between the IDs' efficiency scores on the two verb categories against the same difference in their control group by means of the Bayesian Standardized Difference Test (BSDT, Crawford & Garthwaite, 2007). The BSDT allows obtaining an

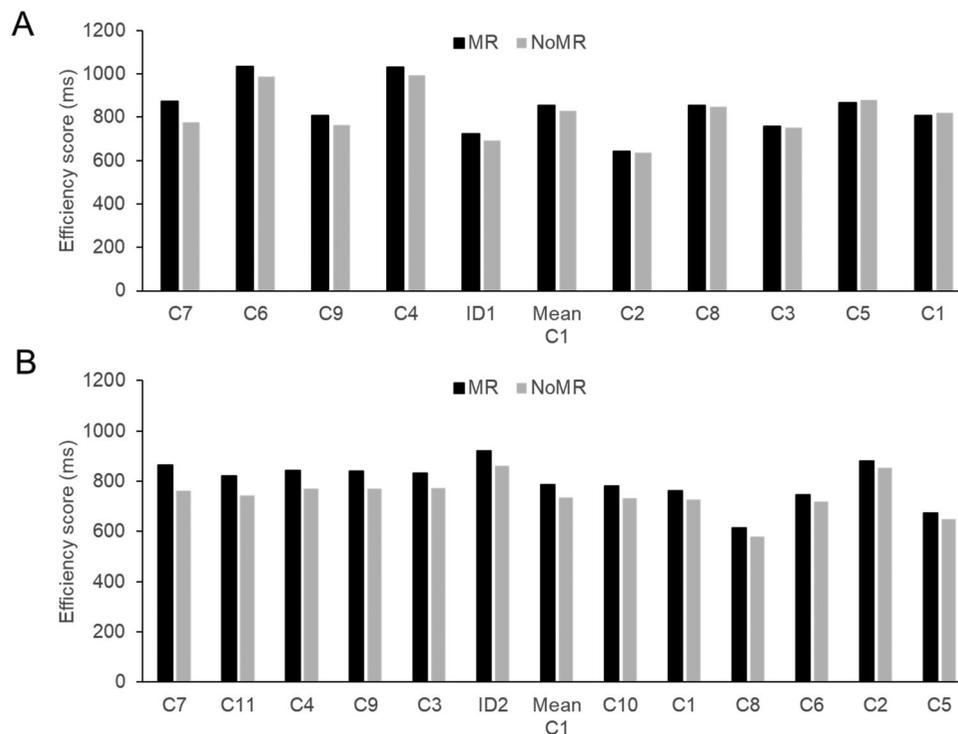


Figure 1. Results. (A) ID1 and his controls' efficiency score for verbs associated with motor representations (MR verbs) and for verbs not associated with motor representations (NoMR verbs). (B) ID2 and her controls' efficiency score for MR and NoMR action verbs. The data are aligned on the x axis in ascending order as a function of the size of the efficiency advantage for the set of MR action verbs (the higher the score the poorer the performance). C = individual control participant. Mean C = average of the control participants.

estimate of the percentage of the control population exhibiting a larger bias than the IDs in favour of the MR verbs and a 95% confidence interval (CI) around this estimate. For ID1, the BSDT indicated that 64% of the population (95% CI = between 27% and 92%) has a larger advantage than ID1 in favour of the verbs associated with motor representations (MR verbs). A similar analysis of ID2's performance indicated that 33% of the population (95% CI = between 4% and 75%) had a larger advantage than ID2 in favour of the MR verbs. Thus, there is no indication that verbs associated with motor representations are processed more efficiently than verbs not associated with motor representations by the IDs, in comparison to the controls' "baseline" performance.

Discussion

Reading action-related words activates parts of the brain known to store motor representations (Fischer & Zwaan, 2008; Willems & Hagoort, 2007). This has led to the view that motor representations constitute an important part of the concepts of action-related words (Gallese & Lakoff, 2005; Pulvermüller, 1999, 2001, 2005). If this view were correct, we would have expected that in a task in which response latencies are influenced by words' conceptual richness (Pexman et al., 2003, 2016) individuals understand words associated with motor representations (i.e., referring to actions that they have performed before) more efficiently than they understand words for actions that are not associated with motor representations. The results reported here do not support this hypothesis. Although our task was sensitive enough to detect effects of words' low level, lexical, and semantic features on participants' response latencies, we detected no advantage in efficiency for action verbs associated with motor representations over action verbs lacking motor representations.

If one accepts that the concreteness judgment task provides a reasonable way to assess the contribution of motor representations in conceptual processing of action-related verbs, then, we can conclude that retrieving motor representations is not necessary for the efficient conceptual processing of action verbs at all. Of course, this assumption may be criticized, and our conclusion may not necessarily generalize beyond the concreteness categorization task. However, there are reasons to believe that the

concreteness judgment task is indeed appropriate to test the predictions of the embodied theory of concepts. First, to our knowledge, this is the only task for which it has been demonstrated that participants retrieve motor representations *during* the stage of conceptual processing, making this task an optimal candidate for testing the contribution of motor representations on conceptual processing of action-related words (Andres et al., 2015). Second, research has shown that this task is particularly sensitive to the richness of semantic representations and, therefore, appropriate to detect an effect of the availability of motor representations in the conceptual processing of action-related words (Pexman et al., 2003, 2016). Pexman and colleagues (Pexman et al., 2003), for instance, examined the processing advantage provided by semantic richness (the number of features associated with a given word) in three semantic decisions tasks (bird/nonbird, living/nonliving and concrete/abstract) and found the largest effect in the concrete/abstract categorization task.

In line with the conclusion reached here, and at odds with the proposal that motor representations constitute an important part of action concepts, many previous studies have reported brain damaged patients who had motor disorders but performed in the normal range of performance in many different tasks assessing conceptual processing of actions such as picture naming, lexical decision and word-picture verification (Bartolo et al., 2001; Chainay & Humphreys, 2003; Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Graham, Zeman, Young, Patterson, & Hodges, 1999; Negri et al., 2007; Ochipa, Rothi, & Heilman, 1994; Papeo et al., 2010; Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008; Pazzaglia, Smania, Corato, & Aglioti, 2008; Rapcsak et al., 1995; Rumiati, Zanini, Vorano, & Shallice, 2001; Tessari, Canessa, Ukmar, & Rumiati, 2007; Vannuscorps et al., 2016). Nevertheless, the interpretation of these findings is somewhat limited by the sensitivity of the tasks and complicated by the difficulty of knowing whether these patients' brain lesion affected their ability to access motor representations and, if so, to what extent. The present study is not subject to these limitations. First, it allowed testing the role of motor representations in conceptual processing of action verbs in individuals who are totally deprived of motor representations for a series of specific, identifiable actions. This avoids the ambiguity of previous studies with brain-

damaged patients as to whether the brain lesion affects the motor representations themselves or, rather, their implementation. Second, our approach allowed testing the contribution of motor representations in a timed task and a within-subject design. These features of the study increase the likelihood of detecting a possible difference between the efficiency of conceptual processing of action-related verbs that are or are not associated with motor representations, in comparison to a baseline constituted by the performance of the control participants who have already performed all these actions. This baseline allows us to exclude that any effect of the contrast between the two categories of hand action verbs in the IDs is due to extraneous factors associated with those verbs since they are the same as those used for the TPs.

The finding that action verbs not associated with motor representations in IDs are understood as rapidly as those associated with motor representations implies that motor representations are not part (or at least not an important part) of action concepts. This finding thus extends those from previous behavioural and neuroimaging studies that showed that the IDs perceive and comprehend hand actions, for which they do not have corresponding effector-specific motor representations, as accurately, as fast, with the same biases, and with the same network of brain areas as typically developed participants (Vannuscorps & Caramazza, 2016; Vannuscorps et al., 2016, 2017; Vannuscorps, Wurm, Striem-Amit & Caramazza, 2019). Those findings imply that efficient perceptual processing of actions does not require effector-specific motor simulation, but left open the possibility that motor representations may nevertheless contribute to the conceptual processing of action verbs, as suggested by proponents of embodied views of conceptual processing (Allport, 1985; Andres et al., 2015; Gallese & Lakoff, 2005; Pulvermüller, 1999, 2001, 2005).

Our finding thus favours a view of the action conceptual system in which conceptual content (e.g., the typical goal, instrument, duration, context, speed or type of movements of an action) is not composed of modality specific representations, but rather of abstract information represented independently from how it has been acquired (Caramazza et al., 1990; Landauer & Dumais, 1997; Tyler & Moss, 2001). Although motor experience could participate in the

acquisition of conceptual knowledge about actions, it is not necessary because its role in concept acquisition is not tied to the acquisition of motor representations, but to the cognitive analysis of motor actions and, therefore, to the acquisition of abstract knowledge about the action, which can also be largely acquired through other modalities. This view of the conceptual system is consistent with the observation that congenitally blind individuals, despite drastically different sensory experiences, acquire largely typical concepts of objects and actions, rely on similar cognitive mechanisms when making semantic judgements about action and object categories, and activate the very same neural mechanisms as sighted people (Bedny & Saxe, 2012; Striem-Amit, Wang, Bi, & Caramazza, 2018).

To be clear, this view of the conceptual system is not incompatible with the possibility that motor representations can, under some conditions or circumstances, affect the processing of action-related words in tasks that involve both conceptual processing and other cognitive processes such as short-term memory or motor imagery. Shebani and Pulvermüller (2013), for instance, provided evidence that rhythmic movements of the hands and the feet during a short-term memory task are associated with greater difficulty in recalling hand-related and foot-related action verbs, respectively. Tomasino and colleagues (Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008) found that TMS applied to the hand area of the primary motor cortex facilitates (leads to faster response latencies) the processing of action verbs in a task requiring motor imagery (from the verb, imagine yourself performing the action. Does it require a hand rotation? Yes/no). Similarly, IDs have difficulties in maintaining information about hand postures for a few seconds in short-term memory (Vannuscorps & Caramazza, 2016). These effects are not problematic for theories which assume that motor representations do not contribute to the conceptual processing of action-related words, because these effects are most likely specific to task demands in memory or imagery operations rather than in conceptual processing per se.

Acknowledgments

We are very grateful to all the participants to this study. We declare that the research was conducted in the absence of

any commercial or financial relationships that could be construed as a potential conflict of interest. This research was supported by the Fondazione Cassa di Risparmio di Trento e Rovereto (Società Mente Cervello), the Provincia Autonoma di Trento and the Harvard Society for Mind, Brain and Behavior.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by Società Scienze Mente Cervello–Fondazione Cassa di Risparmio di Trento e Rovereto, by a grant from the Provincia Autonoma di Trento, and by a Harvard Provostial postdoctoral fund (to A.C.); Harvard Society for Mind, Brain and Behavior.

Ethical approval

The study was approved by the biomedical ethics committee of the Cliniques Universitaires Saint-Luc, Brussels, Belgium and all participants gave written informed consent prior to the study.

Data availability statement

The data that support the findings of this study are openly available in Mendeley Data at <https://doi.org/10.17632/ckn7rd8z69.1>. Reference: Vannuscorps, Gilles (2019), "Conceptual processing of action verbs with and without motor representations", Mendeley Data, v1.

References

- Albani, G., Pignatti, R., Mauro, A., & Semenza, C. (2010). Presence of freezing and naming abilities in Parkinson's disease. *Neuropsychological Trends*, 7, 51–58.
- Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. Newman & R. Epstein (Eds.), *Current perspectives in dysphasia* (pp. 32–60). New York: Churchill Livingstone.
- Andres, M., Finocchiaro, C., Buiatti, M., & Piazza, M. (2015). Contribution of motor representations to action verb processing. *Cognition*, 134, 174–184.
- Bak, T. H., & Hodges, J. R. (2004). The effects of motor neurone disease on language: Further evidence. *Brain and Language*, 89, 354–361.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, 124, 103–120.
- Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., & Hodges, J. R. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, 129, 321–332.
- Balota, D. A., Ferraro, F. R., & Connor, L. T. (1991). On the early influence of meaning in word recognition: A review of the literature. In P. J. Schwanenflugel (Ed.), *The psychology of word meanings* (pp. 187–222). Hillsdale, NJ: Erlbaum.
- Bartolo, A., Cubelli, R., Della Sala, S., Drei, S., & Marchetti, C. (2001). Double dissociation between meaningful and meaningless gesture reproduction in apraxia. *Cortex*, 37, 696–699.
- Bedny, M., & Saxe, R. (2012). Insights into the origins of knowledge from the cognitive neuroscience of blindness. *Cognitive Neuropsychology*, 29, 56–84.
- Bertella, L., Albani, G., Greco, E., Priano, L., Mauro, A., Marchi, S., ... Semenza, C. (2002). Noun verb dissociation in Parkinson's disease. *Brain and Cognition*, 48, 277–280.
- Bestmann, S., Ruff, C. C., Blankenburg, F., Weiskopf, N., Driver, J., & Rothwell, J. C. (2008). Mapping causal interregional influences with concurrent TMS–fMRI. *Experimental Brain Research*, 191(4), 383–402.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15, 527–536.
- Boulenger, V., Mechtouff, L., Thobois, S., Broussolle, E., Jeannerod, M., & Nazir, T. A. (2008). Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns. *Neuropsychologia*, 46, 743–756.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience*, 18, 1607–1615.
- Bub, D. N., Masson, M. E. J., & Cree, G. S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, 106, 27–58.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, 42, 323–334.
- Byrne, R. W. (2003). Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358, 529–536.
- Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology*, 7, 161–189.
- Chainay, H., & Humphreys, G. W. (2003). Ideomotor and ideational apraxia in corticobasal degeneration: A case study. *Neurocase*, 9, 177–186.
- Cortese, M. J., & Fugett, A. (2004). Imageability ratings for 3,000 monosyllabic words. *Behavior Research Methods, Instruments, & Computers*, 36(3), 384–387.
- Cotelli, M., Borroni, B., Manenti, R., Alberici, A., Calabria, M., Agosti, C., ... Cappa, S. F. (2006). Action and object naming in frontotemporal dementia, progressive supranuclear palsy, and corticobasal degeneration. *Neuropsychology*, 20, 558–565.
- Cotelli, M., Borroni, B., Manenti, R., Zanetti, M., Arévalo, A., Cappa, S. F., & Padovani, A. (2007). Action and object

- naming in Parkinson's disease without dementia. *European Journal of Neurology*, *14*, 632–637.
- Crawford, J. R., & Garthwaite, P. H. (2007). Comparison of a single case to a control or normative sample in neuropsychology: Development of a Bayesian approach. *Cognitive Neuropsychology*, *24*, 343–372.
- Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist*, *12*, 482–486.
- Cubelli, R., Marchetti, C., Boscolo, C., & Della Sala, S. (2000). Cognition in action: Testing a model of limb apraxia. *Brain and Cognition*, *44*, 144–165.
- Daniele, A., Barbier, A., Di Giuda, D., Vita, M. G., Piccininni, C., Spinelli, P., ... Gainotti, G. (2013). Selective impairment of action-verb naming and comprehension in progressive supranuclear palsy. *Cortex*, *49*(4), 948–960.
- Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., & Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, *32*, 1325–1341.
- de Zubizaray, G., Arciuli, J., & McMahon, K. (2013). Putting an “end” to the motor cortex representations of action words. *Journal of Cognitive Neuroscience*, *25*(11), 1957–1974.
- Dreyer, F. R., Frey, D., Arana, S., von Saldern, S., Picht, T., Vajkoczy, P., & Pulvermüller, F. (2015). Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions. *Frontiers in Psychology*, *6*, 1161.
- Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the motor system in language comprehension. *Quarterly Journal of Experimental Psychology*, *61*, 825–850.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, *22*, 455–479.
- Gerfo, E. L., Oliveri, M., Torriero, S., Salerno, S., Koch, G., & Caltagirone, C. (2008). The influence of rTMS over prefrontal and motor areas in a morphological task: Grammatical vs. semantic effects. *Neuropsychologia*, *46*, 764–770.
- Glenberg, A. M., & Gallese, V. (2012). Action-based language: A theory of language acquisition, comprehension, and production. *Cortex*, *48*, 905–922.
- Graham, N. L., Zeman, A., Young, A. W., Patterson, K., & Hodges, J. R. (1999). Dyspraxia in a patient with corticobasal degeneration: The role of visual and tactile inputs to action. *Journal of Neurology, Neurosurgery, and Psychiatry*, *67*, 334–344.
- Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., & McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, *71*, 1396–1401.
- Herrera, E., & Cuetos, F. (2012). Action naming in Parkinson's disease patients on/off dopamine. *Neuroscience Letters*, *513*, 219–222.
- Herrera, E., Rodríguez-Ferreiro, J., & Cuetos, F. (2012). The effect of motion content in action naming by Parkinson's disease patients. *Cortex*, *48*, 900–904.
- Heyes, C. M., & Foster, C. L. (2002). Motor learning by observation: Evidence from a serial reaction time task. *The Quarterly Journal of Experimental Psychology Section A*, *55*, 593–607.
- Hodges, J. R., & Bak, T. H. (1997). Noun-verb dissociation in three patients with motor neuron disease and aphasia. *Brain and Language*, *60*, 38–41.
- Howes, D. H., & Solomon, R. L. (1951). Visual duration threshold as a function of word-probability. *Journal of Experimental Psychology*, *41*(6), 401–410.
- Kiefer, M., & Pulvermüller, F. (2012). Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. *Cortex*, *48*, 805–825.
- Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review*, *104*, 211–240.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology-Paris*, *102*, 59–70.
- Mattar, A. A., & Gribble, P. L. (2005). Motor learning by observing. *Neuron*, *46*, 153–160.
- Negri, G. A. L., Rumiati, R. I., Zadini, A., Ukmar, M., Mahon, B. Z., & Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cognitive Neuropsychology*, *24*, 795–816.
- New, B. (2006). Reexamining the word length effect in visual word recognition: New evidence from the English Lexicon Project. *Psychonomic Bulletin & Review*, *13*(1), 45–52.
- New, B., Brysbaert, M., Veronis, J., & Pallier, C. (2007). The use of film subtitles to estimate word frequencies. *Applied Psycholinguistics*, *28*, 661–677.
- Ochipa, C., Rothi, L. J., & Heilman, K. M. (1994). Conduction apraxia. *Journal of Neurology, Neurosurgery & Psychiatry*, *57* (10), 1241–1244.
- Papeo, L., Lingnau, A., Agosta, S., Pascual-Leone, A., Battelli, L., & Caramazza, A. (2015). The origin of word-related motor activity. *Cerebral Cortex*, *25*(6), 1668–1675.
- Papeo, L., Negri, G. L., Zadini, A., & Rumiati, R. I. (2010). Action performance and action-word understanding: Evidence of double dissociations in left-damaged patients. *Cognitive Neuropsychology*, *27*, 428–461.
- Papeo, L., Pascual-Leone, A., & Caramazza, A. (2013). Disrupting the brain to validate hypotheses on the neurobiology of language. *Frontiers in Human Neuroscience*, *7*, 148.
- Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS ONE*, *4*, e4508.
- Pazzaglia, M., Pizzamiglio, L., Pes, E., & Aglioti, S. M. (2008). The sound of actions in apraxia. *Current Biology*, *18*, 1766–1772.
- Pazzaglia, M., Smania, N., Corato, E., & Aglioti, S. M. (2008). Neural underpinnings of gesture discrimination in patients with limb apraxia. *The Journal of Neuroscience*, *28*, 3030–3041.
- Péran, P., Rascol, O., Démonet, J.-F., Celsis, P., Nespoulous, J.-L., Dubois, B., & Cardebat, D. (2003). Deficit of verb generation in

- nondemented patients with Parkinson's disease. *Movement Disorders*, 18, 150–156.
- Pexman, P. M., Heard, A., Lloyd, E., & Yap, M. J. (2016). The Calgary semantic decision project: Concrete/abstract decision data for 10,000 English words. *Behavior Research Methods*, 49, 1–11.
- Pexman, P. M., Holyk, G. G., & Monfils, M.-H. (2003). Number-of-features effects and semantic processing. *Memory and Cognition*, 31, 842–855.
- Pignatti, R., Ceriani, F., Bertella, L., Mori, I., & Semenza, C. (2006). Naming abilities in spontaneous speech in Parkinson and Alzheimer's disease. *Brain and Language*, 99, 124–125.
- Plaut, D. C., & Shallice, T. (1993). Deep dyslexia: A case study of connectionist neuropsychology. *Cognitive Neuropsychology*, 10, 377–500.
- Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences*, 22, 253–279.
- Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, 5, 517–524.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, 11, 351–360.
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, 21, 793–797.
- Rapcsak, S. Z., Ochipa, C., Anderson, K. C., & Poizner, H. (1995). Progressive Ideomotor Apraxia – Evidence for a selective impairment of the action production system. *Brain and Cognition*, 27, 213–236.
- Rodríguez-Ferreiro, J., Menéndez, M., Ribacoba, R., & Cuetos, F. (2009). Action naming is impaired in Parkinson disease patients. *Neuropsychologia*, 47, 3271–3274.
- Rumiati, R. I., Zanini, S., Vorano, L., & Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cognitive Neuropsychology*, 18, 617–642.
- Sandrini, M., Umiltà, C., & Rusconi, E. (2011). The use of transcranial magnetic stimulation in cognitive neuroscience: A new synthesis of methodological issues. *Neuroscience & Biobehavioral Reviews*, 35(3), 516–536.
- Shebani, Z., & Pulvermüller, F. (2013). Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. *Cortex*, 49, 222–231.
- Silveri, M. C., & Ciccarelli, N. (2007). The deficit for the word-class “verb” in corticobasal degeneration: Linguistic expression of the movement disorder? *Neuropsychologia*, 45, 2570–2579.
- Silveri, M. C., Ciccarelli, N., Baldonero, E., Piano, C., Zinno, M., Soleti, F., ... Daniele, A. (2012). Effects of stimulation of the subthalamic nucleus on naming and reading nouns and verbs in Parkinson's disease. *Neuropsychologia*, 50, 1980–1989.
- Spatz, J., Bak, T., Bozeat, S., Patterson, K., & Hodges, J. R. (2002). Apraxia, mechanical problem solving and semantic knowledge: Contributions to object usage in corticobasal degeneration. *Journal of Neurology*, 249, 601–608.
- Striem-Amit, E., Wang, X., Bi, Y., & Caramazza, A. (2018). Neural representation of visual concepts in people born blind. *Nature Communications*, 9(1), 1–12.
- Tessari, A., Canessa, N., Ukmar, M., & Rumiati, R. I. (2007). Neuropsychological evidence for a strategic control of multiple routes in imitation. *Brain*, 130, 1111–1126.
- Tomasino, B., Fink, G. R., Sparing, R., Dafotakis, M., & Weiss, P. H. (2008). Action verbs and the primary motor cortex: A comparative TMS study of silent reading, frequency judgments, and motor imagery. *Neuropsychologia*, 46(7), 1915–1926.
- Townsend, J. T., & Ashby, F. G. (1978). Methods of modeling capacity in simple processing systems. In J. Castellan & F. Restle (Eds.), *Cognitive theory vol. III* (pp. 200–239). Hillsdale, NJ: Erlbaum Associates.
- Townsend, J. T., & Ashby, F. G. (1983). *The stochastic modeling of elementary psychological processes*. Cambridge: Cambridge University Press.
- Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, 5, 244–252.
- Vannuscorps, G. (2019). Conceptual processing of action verbs with and without motor representations, Mendeley Data, v1. <http://dx.doi.org/10.17632/ckn7rd8z69.1>
- Vannuscorps, G., Andres, M., & Pillon, A. (2013). When does action comprehension need motor involvement? Evidence from upper limb apraxia. *Cognitive Neuropsychology*, 30, 253–283.
- Vannuscorps, G., Andres, M., & Pillon, A. (2014). Is motor knowledge part and parcel of the concepts of manipulable artifacts? Clues from a case of upper limb apraxia. *Brain and Cognition*, 84, 132–140.
- Vannuscorps, G., & Caramazza, A. (2016). Typical action perception and interpretation without motor simulation. *Proceedings of the National Academy of Sciences*, 113, 86–91.
- Vannuscorps, G., & Caramazza, A. (2017). Typical predictive eye movements during action observation without effector-specific motor simulation. *Psychonomic Bulletin & Review*, 24, 1152–1157.
- Vannuscorps, G., Dricot, L., & Pillon, A. (2016). Persistent sparing of action conceptual processing in spite of increasing disorders of action production: A case against motor embodiment of action concepts. *Cognitive Neuropsychology*, 33, 1–29.
- Vannuscorps, G., Pillon, A., & Andres, M. (2012). Effect of biomechanical constraints in the hand laterality judgment task: Where does it come from? *Frontiers in Human Neuroscience*, 6, 299.
- Vannuscorps, G. F., Wurm, M., Striem-Amit, E., & Caramazza, A. (2019). Large-scale organization of the hand action observation network in individuals born without hands. *Cerebral Cortex*, 29(8), 3434–3444.
- Watson, C. E., Cardillo, E. R., Ianni, G. R., & Chatterjee, A. (2013). Action concepts in the brain: An activation likelihood estimation meta-analysis. *Journal of Cognitive Neuroscience*, 25(8), 1191–1205.

- Willems, R. M., & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture, and action: A review. *Brain and Language, 101*, 278–289.
- Willems, R. M., Labruna, L., D’Esposito, M., Ivry, R., & Casasanto, D. (2011). A functional role for the motor system in language understanding: Evidence from theta-burst transcranial magnetic stimulation. *Psychological Science, 22*, 849–854.
- Wurm, M. F., & Caramazza, A. (2019). Distinct roles of temporal and frontoparietal cortex in representing actions across vision and language. *Nature Communications, 10* (1), 289.
- Yap, M. J., Lim, G. Y., & Pexman, P. M. (2015). Semantic richness effects in lexical decision: The role of feedback. *Memory & Cognition, 43*(8), 1148–1167.