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A pantomiming priming study on the grasp and functional use actions of tools.

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Abstract

It has previously been demonstrated that tool recognition is facilitated by the repeated visual presentation of object features affording actions, such as those related to grasping and their functional use. It is unclear, however, if this can also facilitate pantomiming. Participants were presented with an image of a prime followed by a target tool and were required to pantomime the appropriate action for each one. The grasp and functional use attributes of the target tool were either the same or different to the prime. Contrary to expectations, participants were slower at pantomiming the target tool relative to the prime regardless of whether the grasp and function of the tool were the same or different – except when the prime and target tools consisted of identical images of the same exemplar. We also found a decrease in accuracy of performing functional use actions for the target tool relative to the prime when the two differed in functional use but not grasp. We reconcile differences between our findings and those that have performed priming studies on tool recognition with differences in task demands and known differences in how the brain recognises tools and performs actions to make use of them.

Introduction

We are constantly using tools such as keys, knives, pens, and other objects throughout our daily lives. The ability to perceive, grasp, and select a functional action to employ with each tool requires a complex series of mechanisms. Certain physical properties of tools, called affordances, influence the way we select an action to apply to a particular tool (Gibson, 1979). For instance, a pair of scissors has certain physical features (e.g. two blades with handles) that afford it being used as a cutting instrument. Considerable research has also demonstrated that even more basic properties, such as an object's shape, size, and weight, can also influence the way we perform actions with tools when using them (Chainay, Brüers, Martin, & Osiurak, 2014; Cuijpers, Smeets, & Brenner, 2004; Tucker & Ellis, 1998).

How a tool is grasped can also determine how we wield it once it is in our hand. For instance, grasping a tool based on the orientation of its handle relative to our bodies affects the movements we select to use it (Creem & Proffitt, 2001; Ellis & Tucker, 2000). In the case of grasping scissors, when the blades are pointing towards us, we typically select an awkward but functional posture to safely grasp the handles. Grasping has been widely studied in both humans and monkeys using various tasks and techniques (Castiello, 2005; Grafton, Arbib, Fadiga, & Rizzolatti, 1996). This work has revealed that non-human primates scale the grip aperture of their grasping hand to match the goal object's physical dimensions (Jeannerod, 1981; Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Napier, 1960; Preuschoft & Chivers, 2012). The processes involved in a successful grasp of an object requires the transformation of the intrinsic properties of the object into an appropriate posture for the grasping hand (Wood, Chouinard, Major, & Goodale, 2017). Processing these object properties has been shown to be done in real-time immediately before the grasp is initiated (Goodale, Jakobson, & Keillor, 1994; Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 2008; Westwood &

Goodale, 2003). This makes sense when we consider that the location of our bodies relative to an object rarely remains static.

The selection of the appropriate action to use a tool as intended, such as grasping scissors by the handles regardless of their position relative to our bodies, requires an understanding of the nature of the object and the current context. Processing this kind of information takes longer than that required for picking up a non-tool given it requires the retrieval of long term conceptual knowledge of how the tool is used (Jax & Buxbaum, 2010; Valyear, Chapman, Gallivan, Mark, & Culham, 2011). As a result, the proper handling of a tool relies on both the processing of visual input on how to configure the hand on the object, which occurs in real-time, and other properties that require the retrieval of conceptual knowledge, which takes longer.

To further explore this area of research, McNair and Harris (2012) used a priming paradigm to investigate whether the grasp (e.g. configuring the hand on the handles of scissors) and the corresponding action associated with a tool (e.g. the snipping of scissors; hereafter called *functional use*) facilitates the subsequent recognition of a different tool with a similar grasp and / or functional use. They presented participants with a picture of a prime followed by a picture of a target tool in which the grasp and functional use could be similar or different. Participants were then asked to identify the tools they saw from an array of different tools presented throughout the study. The authors found that the target tools affording the same grasp as the prime were identified more accurately than those that did not. Conversely, they found that the target tools affording the same functional use as the prime did not present a similar advantage. Based on these findings, the authors concluded that target tools that are preceded by primes affording a similar grasp can facilitate their recognition because the process of selecting grasps is more readily and automatically assessed.

However, similar to a number of studies in this area (Helbig, Graf, & Kiefer, 2006; Kiefer, Sim, Helbig, & Graf, 2011), McNair and Harris (2012) used object identification responses as opposed to a motor task to draw inferences about affordances. This approach is limited in scope because it does not directly examine how the properties of the tools might actually influence real actions. Perhaps a better way to examine this issue is to have participants pantomime the grasp and functional use of tools instead of identifying them verbally. The act of pantomiming consists of performing an action without the physical interaction of an actual tool. As it turns out, functional neuroimaging reveals a common network of brain areas that are engaged when people execute (Hermsdörfer, Terlingen, Mühlau, Goldenberg, & Wohlschläger, 2007), imagine (Grezes & Decety, 2001), and pantomime (Johnson-Frey, Newman-Norlund, & Grafton, 2004) tool-use actions. These mechanisms are complex and entail an interaction between different systems devoted to 1) the perceptual recognition of objects, and 2) the online control of actions (Goodale et al., 1994).

According to Goodale and Milner's Two Visual System Hypothesis (TVSH; (Goodale & Milner, 1992), the processing of visual information for the online control of skilled actions (e.g. reaching and grasping on object) is carried out by the dorsal stream, which includes areas in the posterior parietal cortex that receive projections from the early visual cortex. The processing of visual information for recognition and associating conceptual meaning to stimuli, is driven by the ventral system, which includes visual areas in the inferior temporal cortex that receive projections from the early visual cortex. With this in mind, neuropsychological studies of patients with apraxia underscore the complex nature of these interacting ventral and dorsal systems. Some patients have difficulty selecting actions to perform communicative gestures and pantomiming the use of tools (Goldenberg, 2009; Wheaton & Hallett, 2007) – highlighting the need to investigate how different systems in the brain are involved in processing the perceptual / cognitive and motor-based properties of tools.

According to TVSH, the object identification approach used by McNair and Harris (2012) taps mostly into ventral stream processes, whereas pantomiming tool use taps into both ventral and dorsal processing streams. Although pantomiming does not involve the online control of reaching and grasping actions on a real object, rather, the online control is used to re-enact the grasp and functional use of an imaginary object that is not really there. At the same time, having participants encode different properties of tools and thereafter turn them into motor movements requires the integration of these two visual processing streams. Thus, a pantomiming task could possibly enable one to better examine how the grasp and functional use properties of tools can influence real actions.

The current study used a priming paradigm to investigate how the repeated visual presentation of object features affording grasps and functional use might facilitate pantomiming. We adopted a priming paradigm similar to the one used by McNair and Harris (2012) except we had participants pantomime the action of the prime and target tools as they appeared rather than identifying them from an array afterwards. We asked participants to pantomime the movements to both the prime and target objects as soon as they appeared, rather than having them hold the objects in memory, which would tap into ventral stream processes even more. We hypothesised that pantomiming movements of the second object (target) would be facilitated by the first movement (prime) if it had similar grasp and / or functional use actions. This facilitation, or priming, would be indexed by a decrease in reaction times and an increase in accuracy. The image pairs we used were identical to those used by McNair and Harris (2012), which have already been matched along several nuisance variables by the authors (for more details, see Methods). Using the same set of stimuli also allows one to draw comparisons between our studies more easily. The tools either had a) the same grasp and the same functional use (SGSA), b) the same grasp and a different functional use (SGDA), c) a different grasp and the same functional use (DGSA), d) a different grasp and a different

functional use (DGDA), or e) were identical (SAME). Comparing these conditions allowed us to determine if earlier encounters with tools with similar grasps and / or functional use properties might facilitate pantomiming actions.

Method

Overview

The study included two experimental tasks that differed in stimulus onset asynchronies (SOA). In this study, SOA refers to the amount of time between the onset of the prime and target stimuli. There was a 2-s interval between the prime and target tool in the first task and a 3-s interval between the prime and target tool in the second task. Because typical priming research tends to demonstrate stronger effects with shorter SOAs (Hermans, Spruyt, & Eelen, 2003), the 2-s SOA task was included in an attempt to maximise priming effects while still allowing sufficient time for participants to complete the movements (Hermans et al., 2003). Although this interval turned out to be sufficient, there was nonetheless a concern at the beginning of data collection that this amount of time might potentially be too short for participants to complete the action and return to the starting position naturally. Therefore, we also included a second task with a longer SOA of 3-s. We did not have a fully within-subjects design because we had a limited number of stimuli and wanted to limit the number of times we repeated each one to reduce habituation and maximise our ability to demonstrate priming effects. The 2-s SOA task lasted 35 minutes while the 3-s SOA task lasted 45 minutes. The experimental paradigm is illustrated in Figure 1. An example of a pantomiming movement to a stimulus is displayed in Figure 2.

Participants

Twenty-seven right-handed participants with reported normal or corrected-to-normal vision participated in the study. The 2-s SOA task included 15 participants (7 females, mean age: 24 years, age range: 18 - 44 years) and the 3-s SOA task included 12 participants (7 females, mean age: 26 years, age range: 18- 57 years). Scores ranging from -100 to +100 from the Edinburgh Handedness Inventory (Oldfield, 1971) indicated that 13 participants were strongly right-handed (mean score = 85, range: 61 - 100) while 3 were mildly right-handed (mean score = 46, range: 38 - 53) in the 2-s SOA task. All participants in the 3-s SOA task were strongly right-handed (mean score = 94, range: 76-100). All participants provided written informed consent and all procedures were approved by the Human Research Ethics Committee of La Trobe University in accordance with the Declaration of Helsinki. Participants were compensated for their time with gift vouchers.

Materials and procedure

The stimuli consisted of 40 grey-scale images of tools (200 × 200 pixels, 120 DPI) from the Hemera Technologies Inc. Photo Object Database (Hull, Quebec, Canada). The same stimuli were also used by McNair and Harris (2012). The stimuli were presented as pairs with a ‘prime’ followed by a ‘target’ tool (Figure 1). The presentation order within the pairs of tools was counterbalanced such that each stimulus appeared as often as the prime as it did the target. The image pairs consisted of tools with either the same grasp and same functional use action (SGSA), the same grasp and different functional use action (SGDA), different grasps and the same functional use action (DGSA), and different grasps and different functional use action (DGDA). Finally, there was a fifth condition in which the same tool image was presented as

the prime and target (SAME). The tool pairs across the different conditions were previously matched for grasp, action, shape, and contextual similarities (McNair & Harris, 2012). We used E-Prime 2.0 (Psychology Software Tools, Pittsburg, PA, USA) to present the stimuli on a 15" Dell Precision M6800 laptop computer (Dell Inc., Hopkinton, MA, USA). The participants were seated 40 cm away from the computer screen, which had a resolution of 1024×768 . The stimuli subtended a visual angle of 5.5° .

The experiment began with a small practice session with 10 trials consisting of pairs of tools from the main procedure chosen at random. The main procedure was divided into four blocks (A, B, C and D), each one consisting of 26 trials. The presentation order of the blocks and objects within each block was counterbalanced across participants to control for order effects. The SAME condition was presented 10 times per block (40 trials in total, each trial consisting of a different image). Conversely the other conditions were each presented 4 times per block (16 trials in total for each condition).

The participants were seated comfortably in front of the computer screen with their right elbow on the table. They were instructed to maintain fixation on a central dot, which remained on the screen at all times, and were asked to perform a pantomiming action as quickly and accurately as possible every time they saw an image of a prime or target tool. Between movements, their index finger rested on the first blue button of a Chronos response pad (Psychology Software Tools, Pittsburg, PA, USA). This device was used to measure the reaction time (RT) to initiate a pantomiming action. Specifically, it recorded the time between stimulus onset and the release of the button. As shown in Figure 1, each trial began with the presentation of the prime for 500 ms followed by a mask for 500 ms. This was then followed by a fixation period of 1000 ms for the 2-s SOA task or a fixation period of 2000 ms for the 3-s SOA task. Afterwards, the target tool was presented for 500 ms followed by a mask for 500

ms. Each trial was then followed by a 14-s inter-trial interval (ITI) in which participants continued to maintain central fixation.

We used a Casio EX-FH100 high-speed video camera (Casio Electronic Manufacturing Co., Ltd, Saitama, Japan) to record movements so that we could assess their grasp and functional use accuracy. The field of view was restricted to the participant's hand. The recordings had a temporal resolution of 420 frames per second and a spatial resolution of 224 × 168 pixels. Adobe Premiere Pro software (Adobe Systems Incorporated, San Jose, CA, USA) was used to analyse the recordings offline. The accuracy of each movement was defined as the action we expected participants to make for each tool. This was pre-determined in advance of scoring the videos based on the classifications made by McNair and Harris (2012). The accuracy of the grasp and functional use components for each pantomiming action to either a prime or target tool was evaluated in a binary manner as either 0 for incorrect and 1 for correct. Overall accuracy scores for grasping and functional use actions were then calculated as the percentage of correct responses.

Inter-rater reliability for accuracy scoring

Two raters independently analysed the videos. One rated accuracy for all participants while the other scored a subset of participants (5 participants in the 2-s SOA task and 5 participants in the 3-s SOA task). Both raters were aware of the tool that was presented and the expected response. From their scores, we then calculated the percentage agreement between the number of instances that received the same ratings by both raters. The two raters independently coded 86% grasping and 79% functional use actions in the same manner. The statistics below were performed on the accuracy scores from the first rater who scored all participants.

Statistical analyses

The data were analysed using the Statistical Package for Social Sciences (SPSS) version 23 (IBM Corporation; Armonk, NY, USA), JASP software version 0.8 (University of Amsterdam, Amsterdam, Netherlands), and GraphPad Prism version 6 (GraphPad Software Inc., La Jolla, CA, USA). Three dependent variables were analysed. The first was RT priming for accurate responses only. This measurement was calculated as the percentage change in RT between the prime and target ($((\text{prime object RT} - \text{target object RT}) / \text{prime object RT}) * 100$). The second was the change in grasp accuracy between the prime and target (grasp accuracy for the target – grasp accuracy for the prime). The third was the change in functional use accuracy between the prime and target (functional accuracy for the target – functional accuracy for the prime). The means and standard deviations for RT, grasp accuracy, and functional use accuracy for both the prime and target are also reported.

2×5 analyses of variance (ANOVA) were performed for each dependent variable with SOA (2 levels: 2 s, 3 s) as a between-subject factor and Pantomiming Condition (5 levels: DGDA, DGSA, SAME, SGDA, SGSA) as a within-subject factor. *T*-tests, corrected for multiple comparisons using the Bonferroni method, were performed to further evaluate significant main effects and interactions. One-sample *t* tests, also corrected for multiple comparisons using the Bonferroni method, were performed to determine if RT priming, changes in grasp accuracy, and changes in functional accuracy differed from zero. All reported *p* values represent corrected values unless specified otherwise. Significance was established at an alpha level of .05.

A Bayesian analysis was also performed using the same 2 (SOA) x 5 (pantomiming condition) ANOVA model as above. The Bayes factor we report (BF_{10}) quantified the likelihood that the data supports the alternative relative to the null hypothesis as a ratio between

the two. We considered a BF_{10} value of 3 or above as substantial evidence in favour of the alternative hypothesis and values of 0.33 or less as substantial evidence in favour of the null hypothesis (Jeffreys, 1998). One sample Bayesian t -tests were also performed to determine if RT priming, changes in grasp accuracy, and changes in functional used accuracy differed or not from zero. There was no need to correct for multiple Bayes factors given that they do not reflect probabilities (Gelman, Hill, & Yajima, 2012). The Bayesian analyses allowed us to determine if a different statistical approach might converge with the more traditional ANOVA, which would provide more confidence in the findings, and also draw more definite inferences from null results.

Results

RT priming

In brief, we observed negative priming in all conditions except the SAME condition. In other words, participants were slower to initiate a pantomiming action to a target tool relative to a prime when the two stimuli differed – regardless of whether the two afforded similar grasping and / or functional use actions. Conversely, this interference was not present when the exact same tool was presented twice. This was true for both the 2-s and 3-s SOA tasks. The results are shown in Figure 3. Table 1 provides descriptive statistics for the absolute RT measurements for primes and targets.

Classical ANOVA demonstrated a main effect of Pantomiming Condition ($F_{(4,100)} = 10.20, p < .001, \eta_p^2 = 0.29$). Pairwise comparisons revealed that RT priming in the SAME condition differed from all the other pantomiming conditions (DGDA vs. SAME: $p = .003$, DGSA vs. SAME: $p < .001$, SGDA vs. SAME: $p < .001$, SGSA vs. SAME: $p < .001$). All other

pairwise comparisons did not differ (all $p > .500$). There was no main effect of SOA ($F_{(1,25)} = 1.93, p = .177, \eta_p^2 = 0.07$) nor was there an interaction between Pantomiming Condition and SOA ($F_{(4,100)} = 0.39, p = .813, \eta_p^2 = 0.02$). One-sample classical t -tests revealed that RT priming was lower than zero in all the pantomiming conditions except the SAME condition (DGDA $t_{(26)} = -3.36, p = .002$; DGSA $t_{(26)} = -2.91, p = .007$; SGDA $t_{(26)} = -3.41, p = .002$; SGSA $t_{(26)} = -4.75, p < .001$; and SAME $t_{(26)} = 1.02, p = .324$).

The Bayesian analyses yielded similar results. Bayesian ANOVA demonstrated substantial support for a main effect of Pantomiming Condition ($BF_{10} = 78,169.72$), inconclusive support for or against a main effect of SOA ($BF_{10} = 0.73$), and substantial support against a Pantomiming Condition \times SOA interaction ($BF_{10} = 0.10$). One-sample Bayesian t -tests confirmed the lack of RT priming in the SAME condition ($BF_{10} = 0.32$) and the presence of negative priming in the DGDA ($BF_{10} = 15.78$), DGSA ($BF_{10} = 6.06$), SGDA ($BF_{10} = 17.53$), and SGSA ($BF_{10} = 394.23$) conditions.

Grasp accuracy difference

Figure 4 shows the mean difference in the accuracy of grasp movement scores between the prime and target tools while Table 1 provides descriptive statistics for the absolute accuracy measurements for the primes and targets. In summary, grasp accuracy difference scores did not differ between any of the conditions.

Classical ANOVA revealed no main effect of Pantomiming Condition ($F_{(4,100)} = 0.43, p = .789, \eta_p^2 = .017$), no main effect of SOA ($F_{(1,25)} = 2.58, p = .121, \eta_p^2 = 0.09$), and no Pantomiming Condition \times SOA interaction ($F_{(4,100)} = 2.11, p = .085, \eta_p^2 = 0.08$). Averaging all conditions together and performing a one-sample t -test against zero to determine if there were

any changes in overall accuracy between the prime and target tools revealed no difference ($t_{(26)} = 1.26, p = .221$).

Likewise, the Bayesian ANOVA demonstrated substantial support against a main effect of Pantomiming Condition ($BF_{10} = 0.13$) as well as inconclusive support for or against a main effect of SOA ($BF_{10} = 2.11$) and a Pantomiming Condition \times SOA interaction ($BF_{10} = 2.11$). A one-sample Bayesian t -test comparing the average difference between prime and target tools across all conditions against zero was inclusive ($BF_{10} = 0.413$).

Functional use accuracy difference

Figure 5 shows the mean difference in functional use accuracy between the prime and target tools while Table 1 provides descriptive statistics for the absolute functional use accuracy measurements for the primes and targets. In summary, accuracy diminished when participants pantomimed a target that had the same grasp but a different functional use action than the prime but only in the 3-s SOA task. In other words, performing a different action with a similar grasp causes interference when there is a longer delay.

Classical ANOVA revealed an interaction between Pantomiming Condition and SOA ($F_{(4,100)} = 2.79, p = .030, \eta_p^2 = 0.10$). This interaction was driven by a drop in accuracy in the 3-s relative to the 2-s SOA task in the SGDA condition ($p = .019$). This drop also differed from zero ($p = .015$) and changes in the SGSA condition in the 3-s SOA task ($p = .034$). There were no differences from zero in any of the other conditions (all $p > 0.1$). The main effects of Pantomiming Condition ($F_{(4,100)} = 2.42, p = .054, \eta_p^2 = 0.09$) and SOA ($F_{(1,25)} = 0.08, p = .785, \eta_p^2 = 0.00$) were not significant.

The Bayesian analyses yielded similar results. The Bayesian ANOVA confirmed substantial support for the interaction between Pantomiming Condition and SOA ($BF_{10} = 3.18$),

inconclusive support for or against a main effect of Pantomiming Condition ($BF_{10} = 0.95$), and substantial support against a main effect of SOA ($BF_{10} = 0.24$). One-sample Bayesian t -tests were performed for both the 2-s SOA and 3-s SOA tasks. The 2-s SOA Bayesian t -test revealed inconclusive support for or against a difference from zero in all Pantomiming Conditions; DGDA ($BF_{10} = 0.736$), DGSA ($BF_{10} = 0.734$), SAME ($BF_{10} = 0.345$), SGDA ($BF_{10} = 0.341$), SGSA ($BF_{10} = 2.281$). Additionally, the 3-s SOA Bayesian t -test also revealed inconclusive support for or against a difference from zero in all Pantomiming Conditions; DGDA ($BF_{10} = 0.432$), DGSA ($BF_{10} = 0.380$), SAME ($BF_{10} = 0.623$), SGDA ($BF_{10} = 1.847$), SGSA ($BF_{10} = 0.360$).

Discussion

The present study examined if pantomiming the use of tools can be facilitated by earlier encounters with different tools affording similar grasps and functional use actions. We hypothesised a facilitation in pantomiming when participants performed a second movement that had a similar grasp and / or functional use action as the first, and that this facilitation would reflect a decrease in reaction time and an increase in accuracy. Contrary to this hypothesis, participants took longer to initiate movements to the target tool in all conditions except for the one in which the prime and target were identical. In other words, participants were slower rather than faster at pantomiming the target tool relative to the prime regardless of whether their grasp and functional use were the same or different. We also found a decrease in functional use accuracy for the target tool relative to the prime when the two differed in functional use properties but not in grasp at an SOA of 3-s. Taken together, our results demonstrate an interference in pantomiming two different tools presented in succession, even when they shared similar grasp and functional-use properties.

The question then arises: Why would presenting a different image create interference even when it is supposed to afford a similar grasp and / or functional use? We propose that images intrinsically do not afford these properties in the same way as real objects do. This is not a new idea. As the French surrealist painter René Magritte (1926) pointed out in his *Ceci n'est pas une pipe* (translation: *This is not a pipe*) painting, the image of a pipe is a pictorial representation and not the actual pipe itself. One cannot physically place their hand on the pipe. A three-dimensional structure is required for this purpose. Moreover, the functional use action associated with the pipe is based on a combination of conceptual knowledge and its three-dimensional structure. An alien, naïve to smoking, seeing this painting for the first time may not know what the pipe is for but would perhaps figure it out if a real one was placed in front of them. Thus, this painting provides an example of how two-dimensional images may not necessarily afford grasping or functional use actions in the strictest Gibsonian sense (Gibson, 1979) as there is no way to interact with them physically. If this assertion is correct, then there is a fundamental problem with presenting images or words of tools as a medium for investigating grasping and functional use affordances.

In addition, there is growing evidence demonstrating that the brain processes real objects differently than images of these same objects. For example, using functional magnetic resonance imaging (fMRI), Snow et al. (2011) employed an event-related adaptation paradigm to determine whether neural populations that show repetition suppression for pictures of objects might also show similar responses for real objects. As expected, the authors found strong adaptation to the repetition of pictures of objects in the lateral-occipital complex (LOC). However, adaptation was weaker in this same area when real three-dimensional objects were presented. Given that binocular and oculomotor cues provide useful information about object shape for the latter but not the former, neural populations that process the shape of objects may differ depending on which of these two formats of presentation is used.

Note also that the computations required for physically interacting with a real object are different than those required for pantomiming an action in the air to the image of an object. For one thing, they utilise different spatial frames of reference. The former requires an egocentric frame reference, which is based on spatial coordinates relative to a person's body (Filimon, 2015). According to TVSH, the dorsal stream uses an egocentric frame of reference when configuring a person's hand to the geometrical properties of an object (Goodale & Haffenden, 1998). Namely, the physical structure of the object relative to one's body dictates the way one performs the grasp in real time. This information is missing when a person performs a pantomiming action in the air to a visually presented image – as was the case in our study. A different frame of reference must be used – one that is imaginary and based on some kind of memory. According to TVSH, this would require ventral stream processing in which a perceptual representation is invoked prior to the execution of the action (Foley, Whitwell, & Goodale, 2015). The perceptual analysis of an image is based on a sort of allocentric frame of reference in which the spatial information about different parts of the stimulus is encoded relative to each other as opposed to relative to one's self – and can vary considerably from trial to trial and person to person.

This idea is consistent with evidence from patient D.F. (Whitwell, Milner, & Goodale, 2014) whose ventral stream damage prevents her from pantomiming correctly when asked to show how she would pick up and use an imaginary object. This suggests that she is unable to invoke a perceptual representation of the object in order to engage with it in the absence of tactile confirmation. Conversely, patient D.F.'s successful ability to reach out and grasp objects relies on processes carried out by the visuomotor networks in her dorsal stream. Therefore, we argue that pantomiming the grasp or functional use of an object relies heavily on memory and ventral stream processes.

Neuroimaging evidence from patients with apraxia arising from brain damage further highlight the integral involvement of a fronto-temporo-parietal cortical network in the pantomiming of tool use (Vry et al., 2015). Various researchers share the view that pantomiming tool use is the result of the integration of multiple streams that are essential for specific aspects of higher motor functions (Watson & Buxbaum, 2015). According to TVSH, the ventral stream is critical in selecting actions for tool use given that these actions require the recognition of tools while the dorsal stream is more concerned with the more motoric aspect of these actions (Goodale & Milner, 1992). So, although we have raised some important limitations earlier about pantomiming actions to two-dimensional objects, it does still hold some validity for understanding tool use particularly with regards to action selection. Functional neuroimaging reveals that some of the same brain areas that are engaged in pantomiming tool use are also engaged when participants select actions on real tools (Hermsdörfer et al., 2007). Furthermore, pantomiming tool use is sometimes used clinically to assess if patients might show signs of apraxia (Cassidy, 2016).

Several methodological differences between the present investigation and the McNair and Harris (2012) study should be considered. We had participants respond to both the prime and the target as soon as they each appeared while they had participants match stimuli from an array presented at the end of each trial necessitating memory of the prime and target. We had participants respond to both as they appeared because we wanted to invoke motor representations to the primes to the same extent as when people perform motoric actions. Although we did not find facilitation, there have been a number of studies that have asked participants to respond to both the prime and the target as they each appeared and found strong behavioural priming and fMRI adaptation (Chouinard & Goodale, 2009, 2012; Chouinard, Morrissey, Köhler, & Goodale, 2008; Helbig et al., 2006). Therefore, this methodological difference cannot explain why we obtained interference while McNair and Harris (2012)

obtained facilitation. In addition, McNair and Harris (2012) had a considerably shorter SOA (276 ms) than the SOAs used in our study. We included longer SOAs to allow for sufficient time for participants to perform pantomiming actions to both stimuli. It should be noted that there are a number of studies that have used an SOA of 2 seconds or more and have successfully shown both behavioural priming and fMRI adaptation (Chouinard & Goodale, 2009, 2012; Chouinard et al., 2008; de Groot, Thomassen, & Hudson, 1986). Therefore, the longer SOAs in the present investigation does not explain why we obtained different results than the McNair and Harris (2012) study either. We are left to conclude that differences in results between studies probably arose from a combination of differences between the computational demands required to perform the tasks and differences in time intervals between seeing the stimuli and making a response.

On a different note, our functional use accuracy data revealed a considerable interference effect when participants had to pantomime tools that had the same grasp but a different functional use (i.e. SGDA condition). Namely, they made more errors pantomiming the functional use action of a target when the preceding prime shared the same grasp. This finding suggests that grasps and functional use actions are not fully dissociable from each other and how an object is grasped is an inherent aspect of how it is functionally used. Alternatively, it is also possible that the functional use action to the prime is encoded as a memory trace irrespective of the grasp and that participants might just get stuck on the functional use action (Zhang, Gordon, Fu, & Santello, 2010). Furthermore, this interference effect was much stronger in the 3-s relative to the 2-s SOA. This suggests that a perceptual analysis of the image is required to select a pantomiming movement and that when this analysis is permitted to occur for a longer period of time then the interference effect will be stronger. Thus, the perceptual or semantic analyses of how we can grasp and functionally use objects may also be tightly coupled with each other.

Another methodological issue worth considering is how does one gauge a pantomiming action to be accurate. Selecting an action for a tool depends on context (Johnson-Frey, 2004). For instance, various tools can have more than one associated use. A spoon can be used for stirring soup, if the soup is too hot, or eating, after the soup cooled down. Nonetheless, for scoring purposes, we predetermined what action was expected for each image based on the criteria established in the McNair & Harris (2012) study. All expected actions were based on what they determined to be the most commonly associated action with each particular stimulus. For example, the expected action for a spoon was for eating and not for stirring. This scoring proved to show acceptable validity and reliability. In terms of validity, the mean \pm SD accuracy was $93\% \pm 7\%$ for grasping and $84\% \pm 9\%$ for functional use. In terms of reliability, the two independent scorers showed 86% consistency for the grasp data and 79% consistency for the functional use data. Informing participants in the beginning of the testing session could have improved the reliability of our procedures; however, this would have introduced a memory component to the task. We did not opt for this option because we wanted participants to make the movements as natural as possible.

Given the above, this study provides a cautionary tale that images of objects might be processed differently from real objects and that pantomiming actions to them may involve mechanisms that differ from handling real objects. Further investigation that systematically compares these modalities is required.

Conflicts of interest

All authors declare no conflicts of interest.

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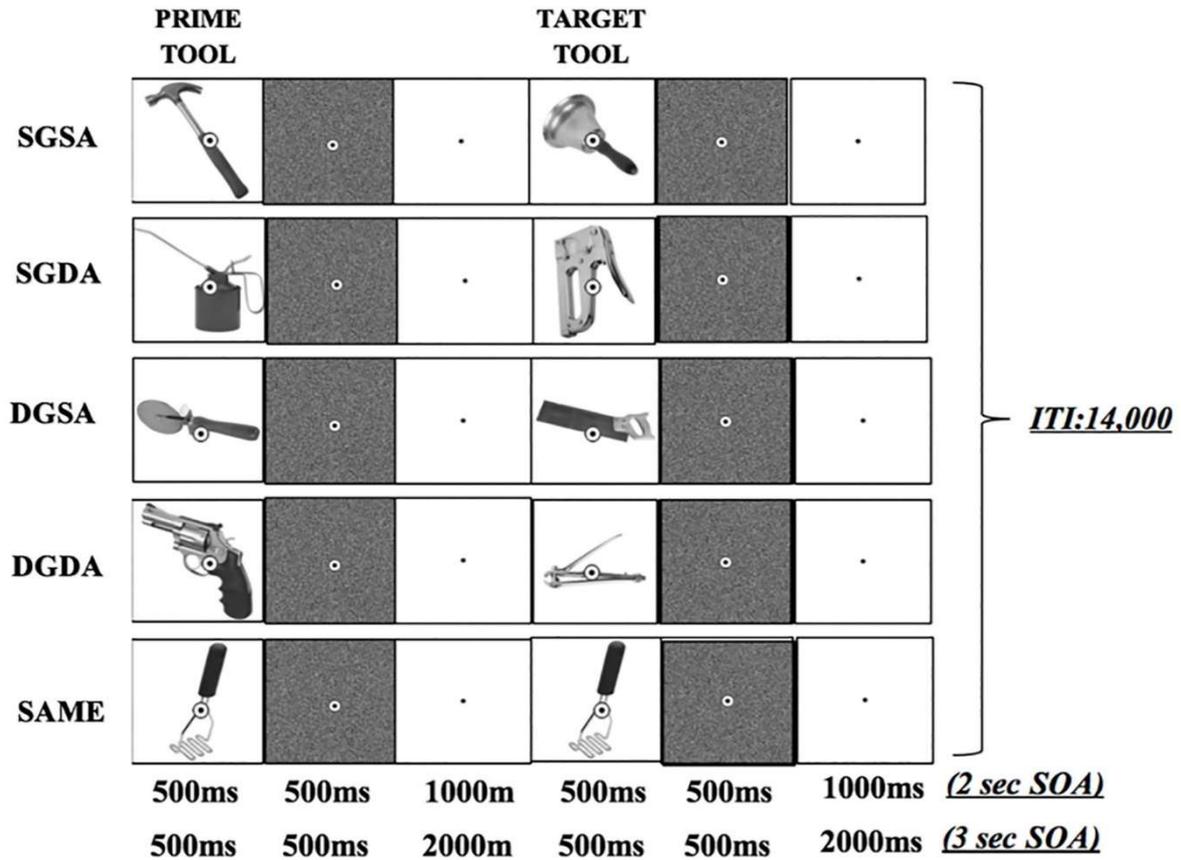


Figure 1. Experimental design and timing parameters. This figure displays examples of pairs of tools used in the different pantomiming conditions: SGSA (same grasp and same functional use action), SGDA (same grasp and a different functional use action), DGSA (different grasp and same functional use action), DGDA (different grasp and different functional use action) and SAME (same image). Each trial included the presentation of the prime tool presented for 500 ms (where participants responded with pantomiming the grasp and functional use action of the tool), followed by a mask for 500 ms, and then by a fixation for 1000 ms for the 2-s SOA and 2000 ms for the 3-s SOA. Thereafter, the target tool was presented for 500 ms (where participants responded by pantomiming the grasp and functional action of the tool again) followed by a mask for 500 ms. Each trial was then followed by a 14-s inter-trial interval (ITI) where participants maintained central fixation. The participants were instructed to perform the actions as quickly and accurately as possible.



Figure 2. Example of an action. The figure provides video frames of a pantomiming action to a photograph of a clothes-peg. ‘Start’ corresponds to the stimulus onset. This was then followed by the pantomiming of the grasp then the functional use action of the tool. ‘Finish’ corresponds to the end of the movement. At the end of the movement, the participant returned their index finger to the response pad and waited for the next stimulus presentation.

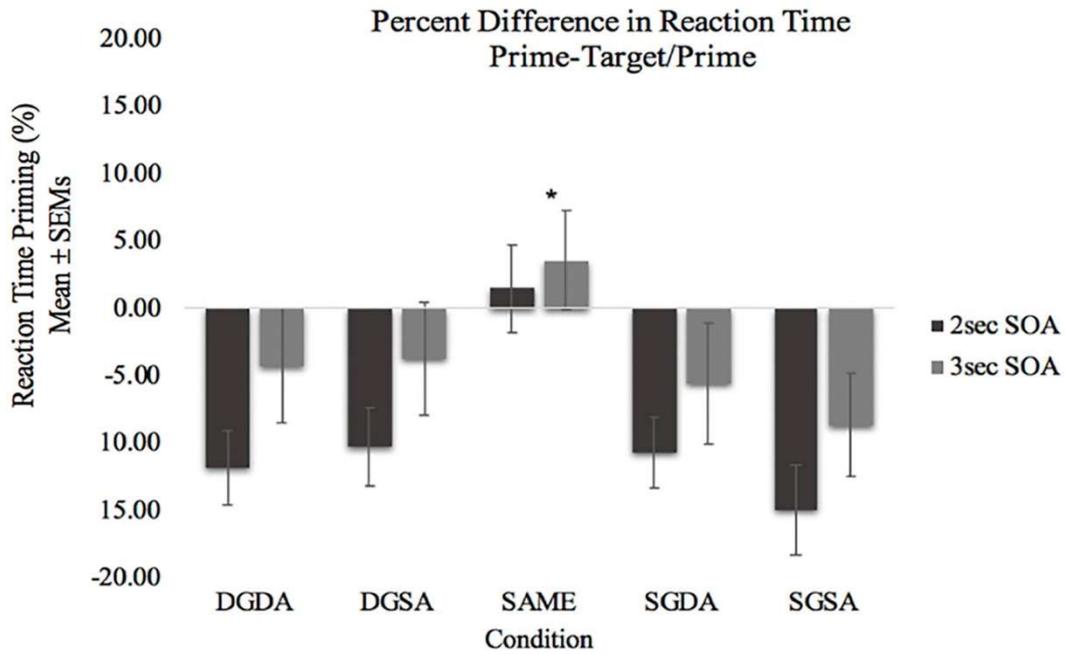


Figure 3. RT priming results. The graph displays the mean \pm SEM RT priming scores in the 2-s (black bars) and 3-s (grey bars) SOA tasks. RT priming was calculated as: (prime tool RT – target tool RT) / prime tool RT * 100. A main effect of Pantomiming Condition was found. Asterisks (*) denotes a significant difference with the SAME condition compare to all the other conditions after correcting for multiple comparisons ($p < 0.05$).

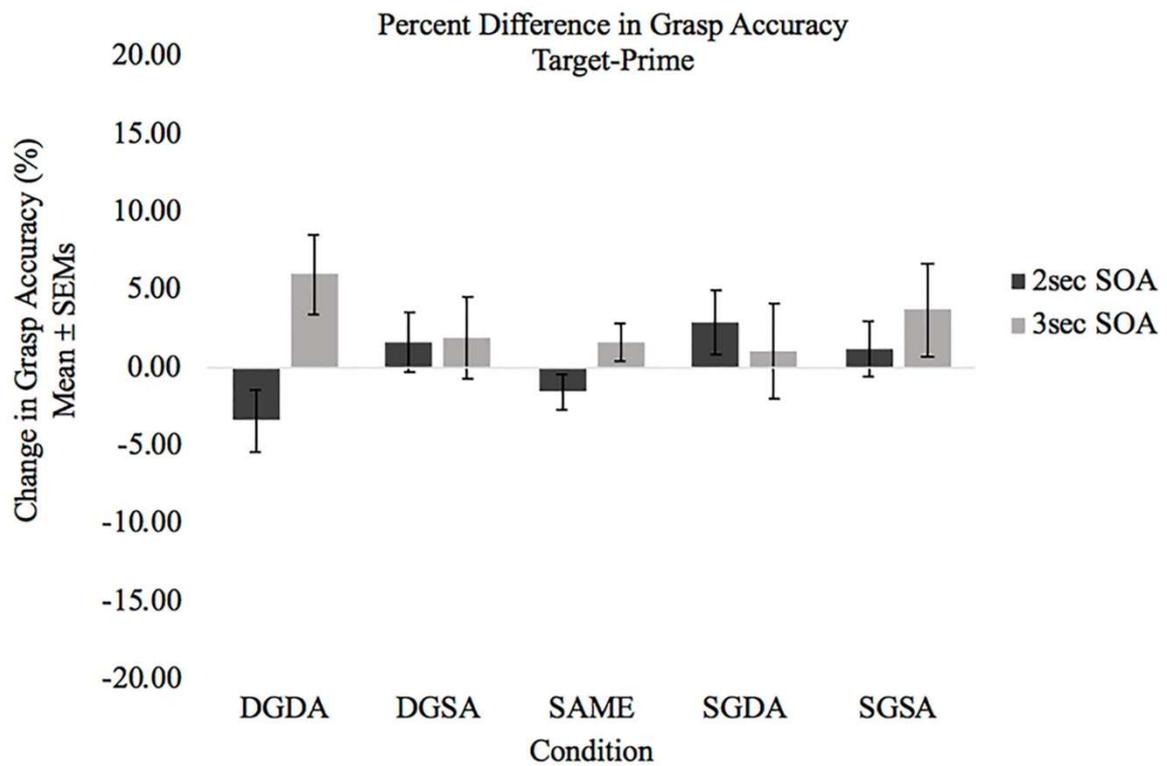


Figure 4. Grasp accuracy difference results. The graph displays the mean \pm SEM percentage of grasp accuracy difference scores in the 2-s (black bars) and 3-s (grey bars) tasks. Grasp accuracy differences scores were calculated as the grasp accuracy for the target tool minus the grasp accuracy for the prime tool. There were no differences between conditions.

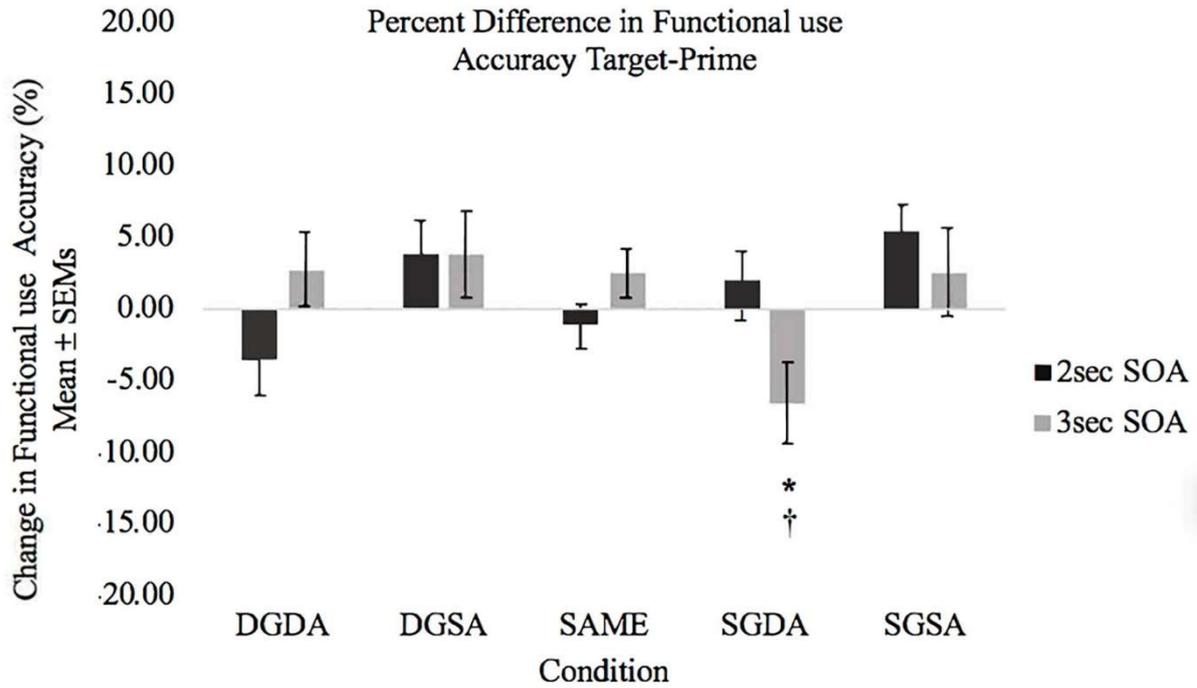


Figure 5. Functional use accuracy results. The graph displays the mean \pm SEM percentage of functional use accuracy scores in the 2-s (black bars) and 3-s (grey bars) SOA tasks. Functional-use accuracy differences scores were calculated as the functional-use accuracy for the target tool minus the functional use accuracy for the prime tool. An interaction between Pantomiming Condition and SOA was found. Asterisks (*) denote a difference between the SAME and SGDA conditions in the 3-s SOA task while a dagger (†) denotes a difference between the 2-s and 3-s SOA task in the SGDA condition after corrections were made for multiple comparisons (both $p < .05$).