Visual and visuomotor processing of hands and tools as a case study of cross talk between the dorsal and ventral streams

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Abstract

A major principle of organization of the visual system is between a dorsal stream that processes visual information in the service of online visuomotor control, and a ventral stream that supports object recognition. Most research has focused on dissociating processing across these two streams. Here we focus on how the two streams interact, and how that interaction may be compromised by damage to structures in the dorsal stream. We tested neurologically-intact and impaired participants in an object categorization task over two classes of objects that depend on processing within both streams – Hands and Tools. We measured how unconscious processing of images from one these categories (e.g., tools) affect the recognition of images from the other category (i.e., hands). Our findings with neurologically-intact participants demonstrated a functional relation between hands and tools – processing an image of a hand hampers the subsequent processing of an image of a tool, and vice versa. These results were not present when we tested apraxic patients (N=3) in the same task; rather if, anything, the apraxic individuals demonstrated a pattern in which tool primes facilitated categorization of hand targets. This finding provides a novel perspective on how the dorsal and ventral streams interact and process visual information, and suggest local and global inhibitory processes working in tandem to co-register information across the two streams.

Keywords: Dorsal stream; Ventral Stream; Apraxia; Hands; Tools; Visual object recognition; Object Use

Introduction

The now classic understanding of how vision works is based on a distinction between two relatively independent streams – the dorsal visual stream and the ventral visual stream (e.g., Goodale & Milner, 1992). These streams process incoming visual information to accomplish complementary computational goals: among other things, the ventral stream is responsible for processing visual information in the service of object identification and perception, whereas the dorsal stream is responsible for extracting object-related volumetric properties (e.g., a 3D description of the object, the object's real-life size) and spatial location in the service of visuomotor interactions with these objects (e.g., Almeida, Mahon, Zapater-Raberov, Dziuba, Cabaço et al, 2014; Cant & Goodale, 2007; Grill-Spector, Kourtzi, & Kanwisher, 2001; Culham, Danckert, De Souza, Gati, Menon, et al., 2003; Goodale & Milner, 1992; Johnson-Frey, 2004; Miceli, Fouch, Capasso, Shelton, Tomaiuolo, et al., 2001; Shmuelof & Zohary, 2005). Consistent with that division of labor, impairments for visually recognizing objects are typically associated with lesions to regions of the ventral stream (e.g., Carey, Harvey, & Milner, 1996; Goodale & Milner, 1992), while difficulties with directing actions toward objects (e.g., grasping) are associated with lesions to dorsal stream areas (e.g., Jeannerod, Decety, & Michel, 1994; Perenin & Vighetto, 1988). A somewhat hybrid type of deficit – apraxia, or the difficulty in manipulating objects correctly or fluidly according to their function – is classically associated with lesions to the inferior parietal lobule, which receives inputs from both the ventral and dorsal visual pathways (e.g., Buxbaum, Kyle, Grossman, & Coslett, 2007; Goldenberg, 2009; Goldenberg & Spatt 2009; Haaland, Harrington, & Knight, 2000; Sirigu, Grafman, Bressler, & Sunderland, 1991; see also Mahon & Caramazza, 2009). Importantly, this division of labor can also be seen anatomically, where the ventral stream projects from primary visual cortex to occipito-temporal and ventral-temporal regions, and the dorsal stream projects to posterior parietal and occipito-parietal regions from primary visual cortex and subcortical structures such as the superior colliculus and lateral geniculate nucleus (e.g., Goodale & Milner, 1992; Lyon, Nassi, & Callaway, 2010; Schmid & Maier, 2015; Schmid, Mrowka, Turchi, Saunders, Wilke et al., 2010; Schmid, Panagiotaropoulos, Augath, Logothetis & Smirnakis, 2009; Sincich, Park, Wohlgemuth & Horton, 2004).

A major focus of research on these streams has been on how they can independently process the incoming visual signal. As such, our understanding of how these two streams interact is still relatively limited. Nevertheless, it is clear that information from these two streams must come into register and interact for optimal object processing. For instance, in order to grasp an object in a functionally appropriate manner, it is necessary to integrate information about object structure (e.g., the handle of the hammer) with volumetric and locational information (the handle is pointed towards the effector; e.g., Almeida, Fintzi, & Mahon, 2013; Arbib, 2008; Brandi, Wohlschläger, Sorg, & Hermsdörfer, 2014; Buxbaum et al., 2007; Chen, Garcea, Almeida, & Mahon, 2016; Garcea, Kristensen, Almeida, & Mahon, 2016; Kristensen, Garcea, Mahon, & Almeida, 2016; Mahon, Kumar, & Almeida, 2013; Peeters, Rizzolatti, & Orban, 2013). Interestingly, when one of the streams is functionally damaged, these different types of information may not be combined in an appropriate manner and performance can be far from optimal. For instance, patient DF presented lesions within the ventral stream and was nevertheless impaired at performing functional grasps (i.e., grasp in order to use) on visually presented objects (e.g., Carey et al., 1996). Specifically, she failed to select the appropriate part of an object to grasp (e.g., the handle) when that part was not pointed directly at her (or her hand). It is also important to note that recent research by Freud and colleagues (e.g., Freud, Culham, Plaut, & Behrmann, 2017; Freud, Ganel, Shelef, Hammer, Avidan et al., 2017; Freud, Plaut & Behrmann, 2016) has emphasized processing of 3D structure of objects for purposes related to perception by regions of posterior parietal cortex that would have classically been considered to constitute part of the dorsal visual pathway.

Here, we focus on how the dorsal and ventral pathways interact in the service of object recognition. We do this by focusing on the visual recognition of two categories for which processing, and perhaps perception and recognition, may depend on processing across *both* streams – *hands* and *tools*.

The development of skilled motor control and tool use was central to our evolutionary past (e.g., Padberg, Franca, Cooke, Soares, Rosa et al., 2007). Hands and tools surely differ in innumerable ways at a sensory/perceptual level—however, despite their differences at a perceptual level, they are tightly linked at a functional level. Ecological and neoecological perspectives on vision and object recognition have long emphasized the importance of this functional relationship (e.g., Gibson, 1979; Tucker & Ellis, 1998). For instance, Gibson (1979) argued that an object within our environment automatically communicates certain action possibilities – *affordances* – that serve to ground functionally adequate behavior. In line with that general idea, it has been demonstrated that in the presence of a (task irrelevant) graspable object, participants are faster to perform hand movements that are compatible with that object's affordance (Bub & Masson, 2010; Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Ellis & Tucker, 2000; Makris, Hadar, & Yarrow, 2011; Phillips & Ward, 2002; Riddoch, Edwards, Humphreys, West, & Heafield, 1998; Riddoch, Humphreys, Edwards, Baker, & Wilson, 2003; Tipper, Paul, & Hayes, 2006; Tucker & Ellis, 1998; Vainio, Ellis, & Tucker, 2007; Vingerhoets, Vandamme, & Vercammen, 2009). Moreover, (task irrelevant) images of hands in particular grasping postures affect object-based decisions (e.g., object categorization), suggesting that the mere observation of a hand with a certain grasp posture activates motor information that can influence the processing of graspable objects (e.g., Borghi, Bonfiglioli, Lugli, Ricciardelli, Rubichi, et al., 2007; Bub, Masson and Lin, 2013; Vainio, Symes, Ellis, Tucker & Ottoboni, 2008). Furthermore, electrophysiological and functional neuroimaging reports have also demonstrated heightened activation of motor, premotor and parietal areas in response to action affordances when viewing hands and manipulable objects (Grèzes & Decety, 2002; Grèzes, Armony, Rowe, & Passingham, 2003; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Valyear, Culham, Sharif, Westwood, & Goodale, 2006). Another set of observations that speak to this issue comes from the examination of mirror and canonical neurons – neurons within the macaque's premotor cortex that respond to the execution and observation of skilled hand movements, or graspable objects, respectively (for a review, see Rizzolatti & Craighero, 2004). Thus, there is clearly a demonstrated functional and neural relation between hands and tools.

Perhaps most intriguing, there are networks of regions selective for tools and hands that lie within the dorsal and ventral streams. Tool items, when compared to items from other categories (e.g., animals), lead to increased neural responses in bilateral superior parietal, dorsal occipital, and medial ventral temporal regions, and left inferior parietal regions, left ventral premotor cortex, and left posterior middle temporal areas (e.g., Almeida, Martins, Bergstrom, Amaral, Freixo, et al., 2017; Almeida et al., 2013; 2017; Chao & Martin, 2000; Chao, Haxby & Martin, 1999; Chen et al., 2016; Freud et al., 2016, 2017a, 2017b; Garcea et al., 2016; Kristensen et al., 2016; Mahon et al., 2013; Mahon, Milleville, Negri, Rumiati, Caramazza et al., 2007; Mruczek, von Loga, & Kastner, 2013; Noppeney, Price, Penny, & Friston, 2006; Peeters, Rizzolatti, & Orban, 2013, for a review see Ishibashi, Pobric, Saito & Lambon Ralph, 2016; Lewis, 2006; Mahon & Caramazza, 2009; Martin, 2007; Orban & Caruana, 2014). Visual perception of hands also elicits stronger responses in dorsal and ventral stream regions, even when compared to other body parts (e.g., Bracci & Peelen, 2013; Bracci, Cavina-Pratesi, Connolly, & Ietswaart, 2016; Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010; Chan, Kravitz, Truong, Arizpe, & Baker, 2010; Desimone, et al., 1984; Kiani, Esteky, Mirpour, & Tanaka, 2007; McCarthy, Puce, Belger, & Allison, 1999; Op de Beeck, Brants, Baeck, & Wagemans, 2010). Specifically, the observation of hands (static or moving) leads to heightened activity in lateral occipital temporal cortex mainly in the left, in aspects of the fusiform gyrus, inferior and superior parietal regions, and premotor, somatosensory and motor regions (Bracci & Peelen, 2013; Bracci et al., 2010; Bracci et al., 2012; Bracci et al., 2016; Grosbas & Paus, 2006; McCarthy et al., 1999; Meier, Aflalo, Kastner, & Graziano, 2008; Op de Beeck et al., 2010; Peeters et al., 2013; Penfield & Boldrey, 1937).

In summary, there is considerable overlap in the neural substrates that mediate perceptual processing of hands and tools, in both the dorsal and ventral streams. Bracci and Colleagues (Bracci et al., 2016; Bracci et al., 2012) demonstrated that some of the areas described above that prefer tools and hands may overlap in a way that is not observed for any other body part or object category; this is particularly true for the left lateral occipital temporal regions, and, perhaps to a less extent, the left anterior intraparietal sulcus. Collectively, the findings briefly reviewed here suggest that functional interactions between tools and hands are supported by dorsal and ventral stream regions. As such, probing how processing hands affects processing tools, and vice versa, holds tremendous promise as a means to further understand how information is processed independently and interactively across the ventral and dorsal visual pathways.

The Current set of Experiments

In two experiments we measured how the processing of one target category (e.g., tools) affected the recognition of the other category (i.e., hands; and vice versa). We presented visual stimuli under conditions of invisibility, and measured how those stimuli affected subsequent conscious decisions about the categorical membership of target objects. We used backward masking to mask the prime pictures and render them invisible to participants. Importantly, we wanted to test how stimuli from the categories of tools and hands influenced each other. As such, for half of the trials, the masked prime pictures could be pictures of hands (or pictures from a companion category – feet), and the target pictures were then pictures of tools (or pictures from a companion category – animals); for the other half of trials, the category membership of the prime and target pictures were reversed. In this way, we tested how the processing of hand/tool pictures (when compared to a control category of foot/animal pictures) affected the categorization of tool/hand pictures.

In a subsequent study (Experiment 3) we used the same experimental paradigm to test three patients who had strokes affecting the dorsal stream, and who had apraxia without corresponding impairments for action recognition or object recognition. By using the same experimental paradigm with these patients, we have the opportunity to ask whether lesions to parietal cortex disrupt interactions between representations of hands and tools.

Experiment 1

Participants performed a simple categorization task on target pictures. These pictures belonged to the categories of tools or animals for half of the trials, and to the categories of hands and feet for the other half of the trials. Participants task was to decide if the picture on every trial was a tool or animal (half of the trials) or a hand or a foot (other half of the trials; categorization decision was blocked, and counterbalanced—see below). Unbeknownst to the participants, each target picture was preceded by an invisibly presented prime picture that could belong to the category of hands or feet, or tools or animals respectively. In order to present the prime pictures and render them invisible we used Backward Masking (e.g., Breitmeyer & Ogmen, 2000; for prior studies from our group using this approach, see Almeida Mahon, Nakayama, & Caramazza, 2008; Almeida et al., 2014). In backward masking, an image is presented for a brief amount of time (e.g., 30 ms) followed immediately by a high contrast random noise mask that renders the image invisible. We measured how long it took to categorize a target picture as a function of the prime presented.

Methods

Participants

Thirty-six undergraduate students participated in the study in exchange for course credit. All participants had normal or corrected to normal vision, were right handed and gave written informed consent. Participants were naive as to the experimental hypotheses. The project was approved by the institutional review board of the Faculty of Psychology and Educational Sciences of the University of Coimbra.

Stimuli

We used pictures of animals, tools, hands and feet found online or that were used in prior experiments (e.g., Almeida et al., 2008). Stimuli were transformed to greyscale and sized to 200 by 200 pixels (see Figure 1). We selected 8 pictures for each category, for a total of 32 pictures. Hand pictures depicted hands (majority of left hands) shaped in two possible grasps (power or precision; equally distributed), and presented in a lateral view, whereas tool pictures were handheld manipulable objects (cleaver, clothespin, hammer, key, scissors, screwdriver, tweezers, and wrench; see Fig. 1). Foot pictures presented right or left feet in different views.

Procedure

Prime pictures were rendered invisible via backward masking. On each trial, a fixation cross was presented in the center of the screen for 500ms and was immediately followed by the prime picture. The prime was presented centrally for 30ms. Then a high contrast backward mask appeared in the same location as the prime picture for 100ms, and was followed by the target picture. The target picture stayed on the screen for 3s or until the participant responded. Participants were instructed to categorize the target stimuli by means of a button press with their right or left index finger (response assignment was counterbalanced across participants) as fast and accurately as possible. For half of the participants, the experiment started with a categorization task over tool and animal stimuli, with hands and feet as primes, whereas for the other half of the participants the experiment started with a categorization task over hand and foot stimuli, with tools and animals as primes. All participants completed both prime/target combinations. Participants were not told that a stimulus was presented before the mask, but were told to pay attention to the center of the screen at all times. There were 64 trials for each prime/target condition, for a total of 512 trials. The experiment lasted approximately forty minutes.

After the experiment proper, participants performed a prime discrimination task that provided independent data on subjects' awareness of the prime. In this task, participants were informed that a prime would be presented and were instructed to categorize the prime pictures into the respective categories. The order of the prime categories (i.e., tools vs animals or hands vs feet) followed the order of the experiment proper. The trial sequence remained the same as in the previous tasks except that the target was not presented.

The monitor refresh rate was 100 Hz. Stimuli were presented using MATLAB and Psychotoolbox (Mathworks Inc., 2013; Kleiner, Brainard, & Pelli 2007).

Analysis

Response times (RTs) were cleaned at the participant level if they were i) below 250 ms (i.e., too fast) or ii) 3 standard deviations above the participant's mean response time across all conditions (i.e., too slow). Cleaned RTs were entered in a 2 (Categorization Decision: hand/feet as targets vs. tool/animal as targets) X 2 (Target Category: hand/tool vs. feet/animal) X 2 (Prime Category: tool/hand vs animal/feet) repeated measures ANOVA. In this ANOVA we were particularly interested in the interaction between Prime Category and Target Category. We then tested simple effects of the priming effects for categorizing the target pictures. Specifically, the RTs for categorizing items from the two categories of interest (Tools and Hands) were inspected on the basis of the category of the prime picture. For tool targets, we compared the categorization time when the prime was a hand (the related category) with the categorization time when the prime was a foot (the unrelated category). For hand targets, we compared the categorization time when the prime was a tool (the related category) with the categorization time when the prime was an animal (the unrelated category). Thus, two hypothesis-driven t-tests were performed to test for category priming – one over the priming effects on the categorization of tool targets, and one over the priming effects on the categorization of hand targets. For completeness, we also tested similar priming effects for the categorization of foot and animal target pictures.

Three a priori criteria were used to exclude participants. First, participants were debriefed at the completion of the prime awareness task; if a participant reported seeing any prime during the experiment proper or prime awareness task, they were discarded without further analysis. No participants were excluded from Experiment 1 for meeting this criterion. Second, a quantitative test of prime awareness was carried out over the prime awareness data, using a z-test for one proportion. Participants whose accuracy in the prime awareness task was significantly different from chance (at $p < .05$) were discarded. No participants were objectively aware of the primes in the prime awareness task (average percent correct performance for prime categorization across all conditions = 50.2%; SEM = 0.2%; critical percent correct performance for above chance categorization calculated from a z-test for one proportion = 58%). Thus, no participants were excluded from Experiment 1 for meeting the criterion of objectively or subjectively seeing the primes. Third, participants with an error rate greater than 2 standard deviations above the mean of the error rate (for the categorization task in the experimental proper) were excluded from further analysis. Six participants were discarded for meeting this criterion. The RTs of the remaining 30 participants were entered in the main analysis.

Results

The RT analysis revealed a significant interaction between Prime Category and Target Category ($F(1,29) = 5.269$, $p = 0.029$). The 3-way interaction between Categorization Decision, Prime Category, and Target Category was not significant ($F < 1$). We then analyzed whether prime pictures of tools and hands affected the categorization of hand and tool targets (see Figure 2A). Reaction times for tool targets were significantly slower in the context of prime pictures of hands than in the context of prime pictures of feet (mean priming effect = -10.4ms, SEM = 4,7ms, t (29) = 2.17, $p < 0.039$; see Figure 2B). A similar interference effect was present when we analyzed the RTs for hand targets: participants were slower to categorize hand pictures in the context of tool primes than in the context of animal primes (mean priming effect = -16.1ms, SEM = 7.2ms, t (29) = 2.20, $p < 0.037$; Fig. 2B). No significant differences were observed for the categorization of foot and animals targets ($t < 1$).

Discussion

Results of Experiment 1 show that there is a privileged functional relation between hands and tools that affects visual recognition: processing an image of a hand hampers the subsequent processing of a tool picture, and vice versa. In order to explore the robustness of this effect, in Experiment 2 we sought to replicate the finding presented in Experiment 1.

Experiment 2

Methods

In Experiment 2 we used the same stimuli, procedure and analysis pipeline as in Experiment 1, and recruited a new group of participants.

Participants

Twenty-five undergraduate students participated in the study in exchange for course credit. All participants had normal or corrected to normal vision, were right handed and gave written informed consent. Participants were naive as to the experimental hypotheses. The project was approved by the institutional review board of the Faculty of Psychology and Educational Sciences of the University of Coimbra.

The same three criteria as used for Experiment 1 were applied for excluding participants in Experiment 2. Three participants were discarded because their error rate was above 2 standard deviations of the mean error rate of all the participants. Four participants were discarded because they were subjectively and/or objectively aware of the prime images (average percent correct performance for prime categorization across all conditions = 50.8%; SEM = 0.9%; critical percent correct performance for above chance categorization calculated from a z-test for one proportion = 58%). The RTs of the remaining 18 participants were entered in the main analysis.

Results

The analysis of the RTs for Experiment 2 revealed an interaction between Prime Category and Target Category ($F(1,17) = 4.260$, $p = 0.055$). The 3-way interaction between Categorization Decision, Prime Category, and Target Category was not significant ($F < 1$). We then analyzed whether prime pictures of tools and hands affected the categorization of hand and tool targets (see Figure 2C). Reaction times for tool targets were slower in the context of prime pictures of hands than in the context of prime pictures of feet (mean priming effect = -6ms, SEM = 2.8ms, t (17) = 2.09, *p* = 0.052; see Figure 2D). A similar interference effect was present when we analyzed the RTs for hand targets, in that participants were slower to categorize hand pictures in the context of tool primes than in the context of animal primes (mean priming effect = -10.4ms, SEM = 4.6ms, *t* (17) = 2.19, *p* < 0.044; Fig. 2D). No significant differences were observed for the categorization of foot and animals targets (*t* < 1).

Discussion

In Experiment 2 we replicated the core finding in Experiment 1. That is, unseen images of tools *hamper* the processing of target (visible) images of hands and *vice-versa*. Importantly, when compared to unrelated categories, the effect obtained in both experiments is one of interference. The interference effects we obtained in Experiments 1 and 2 may open a new window for understanding the functional consequences of neural overlap between tools and hands (Bracci et al., 2012, 2016). At this point it is unclear if the neural overlap observed in fMRI is true neuronal overlap or rather a fine-grained patchiness for tools and hands in the same neural region. Even if there is no direct correspondence in the neuronal representation of hands and tools, close spatial proximity could be associated with lateral inhibition that could explain our behavioral interference effect. Another interesting possibility is that, at least in part, this interference effect may be explained by the fact that hand pictures are perceived as someone else's hands – and not the effectors of the participants. That is, the fulfillment of an object's affordances by the participant might be hindered by the perception of a foreign hand. While the interpretation of our findings must remain speculative at this granularity, the basic finding and inference of a relation between hands and tools in visual processing remains. Finally, the mismatch between the dominant hand of our participants (right-handed), and the majority of the hands depicted on the hand pictures (left hands) may also be an important factor in explaining the result herein. In Experiment 3 we sought to further our understanding of the relation between hands and tools by testing patients with lesions to frontal-parietal areas.

Experiment 3

In Experiment 3 we tested patients with lesions involving parietal cortex, and who exhibited signs of apraxia, in the same experiment as Experiments 1 and 2. The stroke lesions in the participants in Experiment 3 spared ventral stream regions. Thus, each patient could accurately carry out the categorization task over the hand/tool or animal/foot targets (using, presumably, their intact ventral stream). As reviewed in the introduction there is neural overlap for representations of the hands and tools in both the dorsal and ventral streams. If the priming effects observed in Experiments 1 and 2 are supported by processing in parietal areas, or inputs to ventral stream areas from parietal cortex, then a different pattern of priming effects is predicted in the patients than was observed in the healthy controls. Alternatively, if the relation between hands and tools driving the priming effects in Experiments 1 and 2 is supported by processes internal to the ventral stream, then there is no reason why the three patients would not exhibit the same pattern of priming as the healthy controls. In summary, if the patient participants show a pattern of priming distinct from the healthy controls, that would suggest that the priming effects observed in the healthy controls are mediated, in part, by neural overlap between hands and tools in parietal regions.

Methods

Participants

Three patients participated in this experiment. All participants had normal or corrected to normal vision, were right handed and gave written informed consent. Participants were naive as to the experimental hypotheses. The project was approved by the appropriate institutional review board.

Case 1: Patient AA. Patient AA suffered an ischemic stroke in February 2010. At the time of admission he was 47 years-old, was right-handed, and had 13 years of education. He presented with a large lesion in left frontal and parietal cortex, pre/post-central gyrus, and posterior lateral temporal cortex (see Figure 3A; Garcea, Dombovy, & Mahon, 2013). Patient AA was administered a number of tests probing action and object knowledge. Specifically, AA was impaired when instructed to pantomime object use from verbal command and imitate transitive actions, but was at ceiling when imitating intransitive actions. His ability to recognize objects tactilely and explain the function of tools was severely impaired, however, he had no difficulties in matching objects on the basis of their functional similarities, or in naming line drawings of tools and other common objects. While Patient AA was spared when identifying transitive and intransitive actions, he was impaired when matching objects in terms of their manner of manipulation and in retrieving manipulation knowledge of objects. For a detailed description of Patient AA's performance please see Garcea and Colleagues (2013).

Case 2: Patient JT. Patient JT was admitted with an acute ischemic stroke in April 2013. He was 33 years-old at the time of admission, was right-handed, and had 17 years of education. He presented with cortico-subcortical lesions in occipito-parietal areas, the supramarginal gyrus, the intraparietal sulcus and pre-motor regions (see

Figure 3B). Lesions in white matter were also detectable (e.g., centrum semiovale). At the time of admission, Patient JT presented with non-fluent aphasia with spared comprehension, right homonymous hemianopsia, and right hemiparesis from which he recovered almost completely after four days. Other cognitive domains were preserved (e.g., verbal memory and learning, working memory, and executive functions). The study of his praxis abilities included tests that required posture and action imitation, pantomiming of actions from verbal command (transitive and intransitive), and pantomiming of symbolic gestures. He was also assessed for his ability to name actions and objects (the Object and Action Naming Battery; Druks & Masterson, 2000), to match manipulable objects in terms of their associated manipulation and function (Buxbaum & Saffran, 2002), to match objects with related features, and to recognize objects based on tactile input. JT was severely impaired at pantomiming object use from verbal command, and his performance improved when he had to imitate actions or had to use an object (object in hand). His was at ceiling when asked to name objects and actions, recognize objects tactilely and match properties and objects. Finally, he presented difficulties in matching objects based on manipulation knowledge, but not on function knowledge.

Case 3: Patient AB. Patient AB is a right-handed male who was admitted in June 2013 with a two week history of language and writing difficulties and right upper limb weakness. He was 52 year-old at the time of admission and had 9 years of education. Structural MRI (see Fig. 3C) showed a subacute lesion in the left parietal lobule and a smaller lesion in the frontal posterior sulcus. At the time of admission he presented with a mild aphasia with decreased speech output, normal comprehension, and poor repetition of pseudowords (conduction aphasia), a paresis of the right arm and agraphia. Ten days after his first clinical assessment, his speech was fluent with little deficit. To study Patient AB's praxis we followed a similar protocol as the one used for Patient JT. AB was not able to pantomime object use from verbal command; his performance improved slightly when he had to imitate actions, or had to use an object (object in hand). He was at ceiling when asked to recognize objects based on tactile input, match two actions that were semantically related, and match properties (e.g., has wings) with particular objects (e.g., an eagle). Similarly to JT, he presented difficulties in matching objects on manipulation knowledge but had little difficulty when he had to match objects based on function knowledge. Patients JT and AB gave informed consent according to the Ethics committee of the Faculty of Medicine of the University of Lisbon.

Procedure

Experiment 3 used the same materials and followed the same procedure as in Experiments 1 and 2. Stimuli were presented using the software e-prime. All patients were tested in this experiment within a couple of weeks of their neuropsychological assessment to ensure their diagnosis of limb apraxia was still valid. Patient AA completed two sessions of the experiment (data was average between the two sessions), whereas Patients JT and AB completed one session. Patient AA also completed additional studies (not described here).

Analysis

We computed modified one-tailed *t*-tests to assess 1) whether the priming effects for tool and for hand targets in our patients were different from those obtained in Experiment 1 for the control group; and 2) whether those priming effects were different from one another when compared to the same difference in the control group. In Experiments 1 and 2, there was no statistical difference between the priming effects for tool targets and those for hand targets, when those targets were preceded by related primes (i.e., hand or tool prime images respectively). If indeed these effects are differentially dependent on the structures lesioned in our patients (i.e., regions in or around the inferior parietal lobule), then we should expect differences in the priming scores for tool and hand targets for the patient group that are not present for the control group. To that end, we used Crawford and Colleagues' (Crawford & Garthwaite, 2005; Crawford, Garthwaite, & Porter, 2010; Crawford, Howell, & Garthwaite, 1998) Revised Standardized Difference Test (RSDT) to compare differences in the performance of a patient in two tasks with the performance of a control group on the same tasks. Specifically, we compared the priming effects obtain for each patient, with those obtained by the control group. We used the mean priming effects from Experiment 1 (i.e., differences in RTs between the conditions when a target is preceded by a related prime or by an unrelated prime), and the standard error of the mean of the priming effect, and compared those with the individual priming effects of each patient. To aid with visualization of the overall results, we also compared the mean priming effects of interest in the patients to the mean priming effects of interest in controls using the same software. Importantly, the RSDT allows us not only to compare the results for each task with the control group, but the significance of the difference of these results in the patient, compared to controls.

Results

All patients were subjectively and objectively unaware of the presence of the prime pictures (average percent correct performance for prime categorization across all conditions = 51.3%; SEM = 0.03%; critical percent correct performance for above chance categorization calculated from a z-test for one proportion = 58%).

The performance of each patient is presented in Figure 4 (see also Table 1). We compared the priming effects of interest (i.e., tool and hand targets) for each patient with those of the neurologically-intact individuals in Experiment 1. We first compared each individual patient with the controls for each specific priming effect (e.g., the priming effect over hand targets). The difference in priming effect for hand targets between each patient and controls was significant for each patient (Patient AA: priming effect = 36 ms, t (29) = 7.31, p < 0.00001; Patient JT: priming effect = 17 ms, t (29) = 4.64, p = 0.00003; Patient AB: priming effect = 13 ms, t (29) = 4.08, p = 0.00016). Notably, all patients presented a positive priming effect (Fig. 4B), contrary to what was obtained in Experiments 1 and 2. This was not true for the priming effects for tool targets (Patient AA: priming effect = -22 ms, t (29) = -2.36, p = 0.013; Patient JT: priming effect = -10 ms, t < 1; Patient AB: priming effect = 30 ms, t (29) = 7.87, p < 0.00001), where there were mixed results. Furthermore, the differences between the priming effects for each patient were different from those obtain in Experiment 1 for neurologically-intact participants (Patient AA: t (29) = 6.77, p < 0.00001; Patient JT: t (29) = 3.26, p = 0.00281; Patient AB: t (29) = 2.67, p = 0.012). As can be seen in Figure 4 (and most prominently Fig. 4B), while the priming effects for hand targets were relatively stable, that is not the case for the priming effects for tool targets. This is mirrored in the statistical tests performed to measure how different the mean priming effects were between participants and controls using RSDT (patient's mean priming effects for hand targets = 22 ms, SEM = 7 ms, t (29) = 5.34, p < 0.00001; patient's mean priming effects for tool targets = -1 ms, SEM = 16 ms, t (29) = 1.77, p = 0.044). That is, priming effects obtained for the patients were different from those of the neurologically-intact participants. Moreover, priming for hand targets was considerably above zero, whereas priming for tool targets was close to zero. Moreover, the difference between those mean priming effects for patients was different than the difference for neurologically-intact participants (t (29) = 2.51, p < 0.018).

Discussion

Experiment 3 evaluated whether the priming effects for tool and hand targets observed in healthy participants (Experiments 1 and 2) were altered by lesions to parietal cortex, and the presence of apraxia. We found that the patient participants exhibited effects of tool primes on the categorization of target hand pictures, but did not show consistent effects of hand primes on the categorization of target tool pictures. A central interpretation of this asymmetry between the effects of tool processing on the categorization of an hand image, and the (lack of) effects of hand processing on the categorization of a tool is that the effect of hand primes on tool targets depends on processing in parietal cortex.

Another interesting aspect of the results from Experiment 3 is the fact that, contrary to the priming effects obtained in Experiments 1 and 2, in the patient participants, tool primes if anything facilitated the categorization of hand targets. This switch from interference (in Experiments 1 and 2) to facilitation may be related to damage to parietal structures, and by hypothesis, an absence of competing interpretations of the visual input that may be typical of the interplay between dorsal and ventral streams in neurologically-intact individuals.

Experiment 3 has limitations that warrant caution when interpreting the results. First, we cannot know on the basis of the current data which of the several cognitive impairments the patients exhibited was critical for disrupting the typically observed pattern of priming effects. For instance, while we have emphasized the assumption that patients had disrupted ability to demonstrate object use, the source of the discrepant priming effects could have more to do with object grasping than object manipulation. Second, the analysis of the patient data is complex given the limited number of participants (N=3), and the type of data that was obtained (priming effects). Although the use of reaction time approaches in (cognitive) neuropsychology is an important and potentially powerful means to study subtle effects of cognitive deficits or brain lesions, it also brings with it a number of analytic issues. Nevertheless, it seems an interesting approach to be used in tandem with more traditional cognitive neuropsychological approaches (e.g., Buxbaum & Saffran, 2002; Buxbaum et al., 2007; Caramazza & Shelton, 1998; Carey et al., 1996; Garcea et al., 2013; Goodale & Milner, 1992; Jeannerod et al., 1994; Marques, Raposo & Almeida, 2103; Miceli et al, 2001; Negri et al, 2007; Perenin & Vighetto, 1988; Riddoch et al., 1998, 2003; Stasenko, Bonn, Teghipco, Garcea, Sweet, et al., 2015). For these reasons, we consider the results of Experiment 3 to be more suggestive than decisive, and that they motivate a more comprehensive study of this issue, ideally with a larger number of patients with parietal lesions.

General Discussion

In a series of studies we sought to test how processing across the dorsal and the ventral visual pathways interacts in support of processing of high-level object properties. In particular we focused on the categories of tools and hands, as these two categories provide an important window into dorsal/ventral stream interactions. This is because both types of stimuli differentially engage structures within the two streams. We tested how unconsciously presented prime pictures from one of the categories (e.g., hands) influenced the overt categorization of the other category (e.g., tools) in both neurologically-intact and in participants with lesions involving parietal cortex.

Our data show that unconscious processing of tools and hands influences recognition of hand and tool stimuli respectively. Specifically, in Experiments 1 and 2 neurologically-intact participants were slower to categorize hands and tools in the context of tool and hand primes, respectively, than in the presence of unrelated prime stimuli. However, when we tested neurologically-impaired participants with deficits in object manipulation due to lesions within frontal-parietal regions (e.g., Buxbaum et al., 2007; Haaland et al., 2000; Goldenberg & Spatt 2009), an effect of the prime on subsequent categorization was restricted to when pictures of tool primes preceded the categorization of hand stimuli. Importantly, this effect was no longer an interference effect (as those obtained with neurologically-intact participants in Experiments 1 and 2) but was rather one of facilitation.

The results we have reported suggest that putative neural overlap observed between hand-preferring and tool-preferring regions in dorsal and ventral visual stream structures (Bracci et al., 2012, 2016) may be dependent on different, and perhaps complementary, types of information. In Experiments 1 and 2, the categorization of both types of targets was *hampered* by prime pictures from the other category, whereas in Experiment 3 only the categorization of hands was influenced by prime pictures. The performance of the patients participants suggests that the effect of hands on tools may be more dependent on processes occurring in frontal-parietal areas (e.g., Brandi et al, 2014; Peeters et al., 2013), whereas the influence of tools on the processing of hands is relatively independent of processing occurring in dorsal regions. Presumably then, information conveyed by hand stimuli can be used by the system when processing aspects of tool knowledge related with object manipulation and object use.

The results reported herein may shed light on the nature of the neural overlap across the two streams for processing tools and hands. One possible explanation for these interference priming effects is that the putative neural overlap between the processing of tools and hands in both streams is a byproduct of fine-grained patchiness for tools and hands in the same neural region, and not so much true 'neuronal' overlap. For instance, work with non-human primates has suggested that some face and body patchiness can be masked by apparent neural overlap when using fMRI (e.g., Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). Thus, potentially adjacent but nonoverlapping hand and tool patches could have lateral inhibitory connections, which might explain the interference effects that we observed in Experiments 1 and 2. An alternative explanation could be that the presence of a picture of someone else's hand may inhibit the preparation of an affordance-driven motor program. In fact, Oosterhof and Colleagues (Oosterhof, Tipper, & Downing, 2012) demonstrated that first-person and third-person perspectives may be differentially processed in the context of preparing motor programs toward objects. Given that the pictures of hands presented in our experiments are not the participants' own hands, and are not presented in first-person view, these pictures could potentially interfere with the processing of affordance-driven motor programs, and hence lead to interference effects. Moreover, most of the hands depicted are left hands, whereas all our participants were right-handed – this mismatch between handedness and prime hand could also be germain to understanding the cause of the interference effects we observed. Note, however, that this may not be able to explain the inverse effects observed in Experiment 3.

Our findings suggest a new approach for studying the representation of hands and tools in the brain. In neurologically-intact participants (i.e., Experiments 1 and 2), our priming effects are of interference – that is, the processing of one of the categories disturbs the processing of the other category. In the patient participants (Experiment 3), the effect of the prime was one of facilitation – categorizing hands benefits from a preview of a tool item. While the two possibilities presented above may explain (together or independently) the interference effects obtained in Experiments 1 and 2, they may not be sufficient to explain the shift from interference to facilitation in Experiment 3. The finding that hands no longer influence the processing of tools in the setting of frontal-parietal lesions, while tool primes facilitate the processing of hands, may suggest that the interference effect is dependent on inputs from frontal-parietal areas on ventral stream processing of those categories.

It is important to note that the 3 experiments presented have a set of limitations that may need to be addressed in future experiments. For instance, it may interesting to see if the results of Experiments 1 and 2 can be replicated under situations where the primes are depicted in a first person perspective and are aligned with the handedness of the participants. It may also be important to test a more extended number of patients such that the analytical pipeline used for Experiments 1 and 2 can also be applied to a group of patients. Finally, the healthy young (psychology undergraduate) participants from Experiments 1 and 2 were not matched in gender to our patients. Nevertheless, in our previous publications (e.g., Almeida, Mahon, Caramazza, 2010; Almeida et al., 2008) we showed that these groups of individuals present typical tool priming effects, suggesting that the effect of gender in tool priming may be small (if at all).

Another aspect that is worth mentioning refers to whether these effects are limited to tools in a strict sense, or whether they are more generally related to the processing of a graspable object. The stimuli we use in our experiments may already be consider has non-complaint to a strict definition of what a tool is. Most importantly, we and others have shown before that one aspect that may drive these types of effects relates to object elongation as a proxy for graspability (e.g., Almeida et al., 2014; Fabbri, Stubbs, Cusak, & Culham, 2016). As such, the unique relationship between the processing of hands and tools concerns a broad definition of tools that includes graspable objects, and perhaps particularly those that are elongated.

More broadly, the findings we have reported underline the importance of testing neurologically-impaired participants and neurologically-intact participants in parallel psychophysical experiments, in parallel to the neuropsychological approaches typically used. Future work in this line could capitalize on pairing functional neuroimaging with psychophysical manipulations to study how brain lesions may alter processing in anatomically remote but functionally connected regions.

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Figures

Figure 1

Figure 2

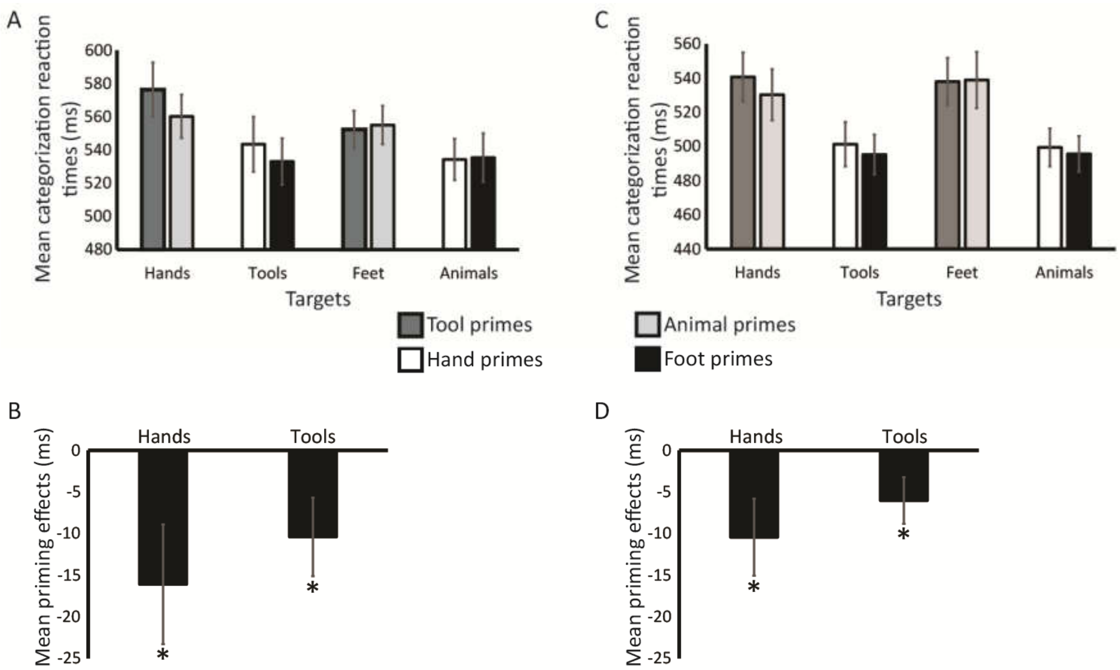
A
Mean categorization reaction times (ms)
600
580
560
540
520
500
480
Hands
Tools
Feet
Animals
Targets
Tool primes
Hand primes
C
Mean categorization reaction times (ms)
560
540
520
500
480
460
440
Hands
Tools
Feet
Animals
Targets
Animal primes
Foot primes
B
Mean priming effects (ms)
0
-5
-10
-15
-20
-25
Hands
Tools
*
*
D
Mean priming effects (ms)
0
-5
-10
-15
-20
-25
Hands
Tools
*
*

Figure 3

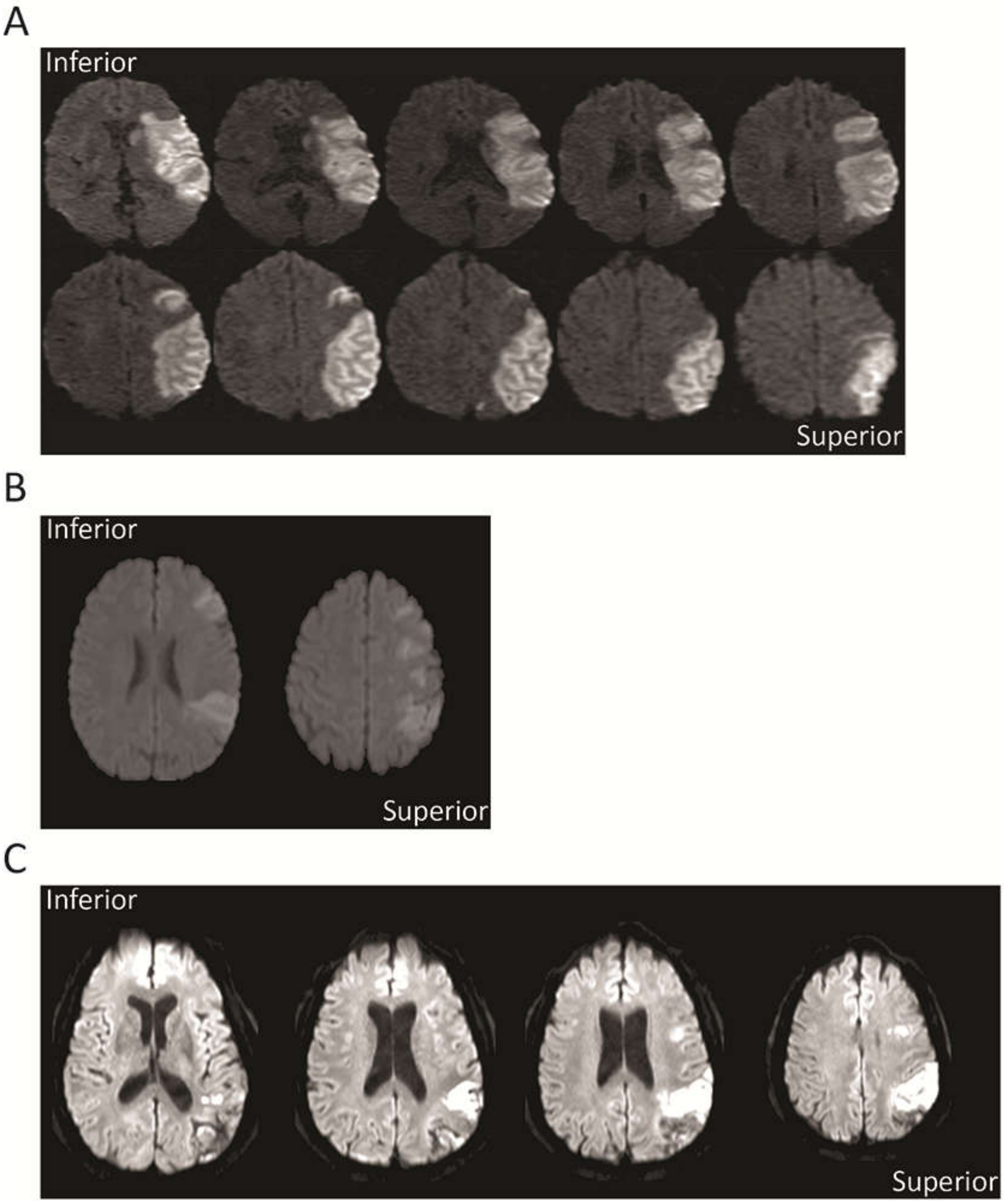
A
Inferior
Superior
B
Inferior
Superior
C
Inferior
Superior

Figure 4

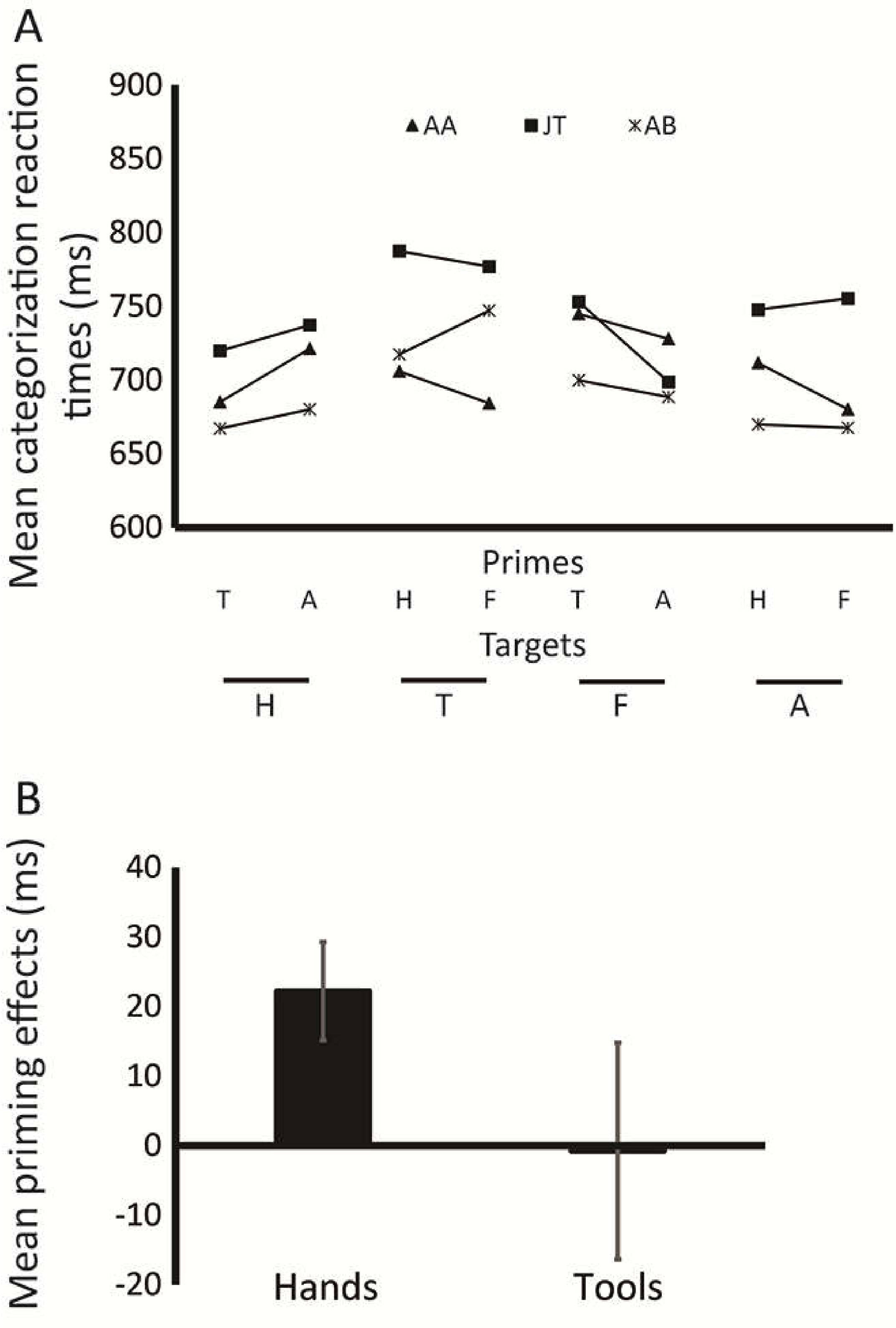
A
Mean categorization reaction times (ms)
900
850
800
750
700
650
600
▲AA
■JT
✳AB
Primes
T A H F T A H F
Targets
H
T
F
A
B
Mean priming effects (ms)
40
30
20
10
0
-10
-20
Hands
Tools

Figure Legends

Figure 1. Stimuli used in the experiments. In this figure we present all the stimuli used in Experiments 1 – 3.

Figure 2. Priming results for Experiments 1 and 2. (A) Mean categorization times by target and prime category for Experiment 1. (B) Mean priming effects for the categorization of the categories of interest (i.e., Hands and Tools) for Experiment 1. (C) Mean categorization times by target and prime category for Experiment 2. (B) Mean priming effects for the categories of interest for Experiment 2. Error bars represent the standard error of the mean (SEM) across participants. * for $p < 0.05$.

Figure 3. Lesion sites for Patients AA, JT, and AB. MRI scans for the three patients. (A) DWI scan for Patient AA. (B) DWI scan for Patient JT. (C) DWI scan for Patient AB.

Figure 4. Response times for the patient participants in Experiment 3. (A) Mean mean categorization times by target and prime category for each patient in Experiment 3. (B) Mean priming effects of interest for the patient participants.

Table 1.

Reaction times for the three patients and the average of the neurologically-intact individuals per condition of interest

Target		Tool	Tool	Hand	Hand
Prime		Hand	Foot	Tool	Animal
Patients	AA	705.9	684.3	685.2	721.3
	JT	787.4	777	719.9	737.2
	AB	717.4	747.1	667.2	680.2
Controls (Experiment 1)		543.4 (90.6)	533 (76.9)	576.3 (89.4)	560.2 (71.6)

Note: Reaction times in ms; Standard deviation of the control participants in parentheses