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Abstract

Comparison between real and pantomimed actions is used in neuroscience to dissociate stimulus-driven (real) as compared to internally driven (pantomimed) visuomotor transformations, with the goal of testing models of vision (Milner & Goodale, 1995) and diagnosing neuropsychological deficits (apraxia syndrome). Real actions refer to an overt movement directed toward a visible target whereas pantomimed actions refer to an overt movement directed either toward an object that is no longer available. Although similar, real and pantomimed actions differ in their kinematic parameters and in their neural substrates. Pantomimed-reach-to-grasp-actions show reduced reaching velocities, higher wrist movements, and reduced grip apertures. In addition, seminal neuropsychological studies and recent neuroimaging findings confirmed that real and pantomimed actions are underpinned by separate brain networks. Although previous literature suggests differences in the praxis system between males and females, no research to date has investigated whether or not gender differences exist in the context of real versus pantomimed reach-to-grasp actions. We asked ten male and ten female participants to perform real and pantomimed reach-to-grasp actions toward objects of different sizes, either with or without visual feedback. During pantomimed actions participants were required to pick up an imaginary object slightly offset relative to the location of the real one (which was in turn the target of the real reach-to-grasp actions). Results demonstrate a significant difference between the kinematic parameters recorded in male and female participants performing pantomimed, but not real reach-to-grasp tasks, depending on the availability of visual feedback. With no feedback both males and females showed smaller grip aperture, slower movement velocity and lower reach height. Crucially, these same differences were abolished when visual feedback was available in male, but not in female participants. Our results suggest that male and female participants should be evaluated separately in the clinical environment and in future research in the field.

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Comparison between real and pantomimed actions is used in neuroscience to dissociate stimulus-driven (real) as compared to internally driven (pantomimed) visuomotor transformations, with the goal of testing models of vision (Milner & Goodale, 1995) and diagnosing neuropsychological deficits (apraxia syndrome). Real actions refer to an overt movement directed toward a visible target whereas pantomimed actions refer to an overt movement directed either toward an object that is no longer available. Although similar, real and pantomimed actions differ in their kinematic parameters and in their neural substrates. Pantomimed-reach-to-grasp-actions show reduced reaching velocities, higher wrist movements, and reduced grip apertures. In addition, seminal neuropsychological studies and recent neuroimaging findings confirmed that real and pantomimed actions are underpinned by separate brain networks. Although previous literature suggests differences in the praxis system between males and females, no research to date has investigated whether or not gender differences exist in the context of real versus pantomimed reach-to-grasp actions. We asked ten male and ten female participants to perform real and pantomimed reach-to-grasp actions toward objects of different sizes, either with or without visual feedback. During pantomimed actions participants were required to pick up an imaginary object slightly offset relative to the location of the real one (which was in turn the target of the real reach-to-grasp actions). Results demonstrate a significant difference between the kinematic parameters recorded in male and female participants performing pantomimed, but not real reach-to-grasp tasks, depending on the availability of visual feedback. With no feedback both males and females showed smaller grip aperture, slower movement velocity and lower reach height. Crucially, these same differences were abolished when visual feedback was available in male, but not in female participants. Our results suggest that male and female participants should be evaluated separately in the clinical environment and in future research in the field.

1. Introduction

What makes a good mime artist seem to really be banging on an invisible wall? How does an actor in a film appear natural while fighting against a computer generated creature, and how does a magician convince us that a coin has been picked up and is about to 'vanish' for the next trick? What these people have in common is the ability to interact with imaginary objects, yet still produce movements that accurately portray, down to the fine details, the way we would expect to see someone move when the objects they are handling are actually there (Sito, 2013) These fine abilities of experts in action miming are quite surprising given that it is now well documented that humans move quite differently when asked to perform a real goal directed action, for example picking up an apple, as compared to its relative pantomimed action of picking up an imaginary apple.

Comparisons between performing real and pantomimed actions have been used in the field of neuroscience to dissociate stimulus driven (used in real action) as compared to internally driven (used in pantomimed action) visuomotor transformation with the goals (among others) of diagnosing neuropsychological disorders such as ideomotor apraxia (Sunderland & Shinner, 2007) and of testing models of vision (Milner & Goodale, 1995). In both instances, most studies used movements of the upper body, with a particular attention to grasping actions and tool use. The terms "pantomime" and "pantomimed action" is used in this context to describe actions performed toward 3-dimensional objects that are not actually physically present. This condition has been experimentally tested in different laboratories by using virtual representations (Santello, Flanders, & Soechting, 2002), mental images (Goodale, Jakobson, & Keillor, 1994), remembered items (Milner et al., 2001), or not-graspable two-dimensional images (Westwood, Danckert, Servos, & Goodale, 2002)

In neuropsychology, the ability to skilfully use tools - for example using a pair of scissors to cut a piece of paper - is clearly dissociated from the ability to pantomime the use of scissors: patients with lesions within the fronto-parietal network can perform the former task relatively well, but not the latter (Goldenberg, 2009; Goldenberg & Spatt, 2009). In this particular context, the use of pantomimed actions has suggested to neuropsychologists that the fronto-parietal brain areas usually lesioned in patients with ideomotor apraxia might play a key role in converting mental images of well learned actions into their corresponding motor execution. Behavioural studies (Hermsdorfer, Li, Randerath, Goldenberg, & Johannsen, 2012; Hermsdorfer, Li, Randerath, Roby-Brami, & Goldenberg, 2013) have demonstrated a

high correlation between the kinematics parameters recorded while participants were performing pantomime tasks (reproducing the action of scooping with the hand) and demo tasks (reproducing the action of scooping using a spoon). Importantly, weak correlations were instead recorded when both pantomime and demonstration tasks were compared to actual use task (using a spoon to scoop soup for real). Interestingly, patients with apraxia behaved similarly to controls, with the difference that the former appeared to have more problems with specific movements such has wrist rotation. The severity of the deficit was seen to decrease along a gradient from pantomime, to demo, to use tasks (Hermsdorfer, et al., 2013; Laimgruber, Goldenberg, & Hermsdorfer, 2005)

Differences between real and pantomimed grasping actions have also been used to support the theory that different pathways in the primate brain sustain vision for action and vision for perception (Goodale & Milner, 1992; Goodale & Westwood, 2004). According to this model, the ventral stream in the occipito-temporal cortex transforms visual information into durable perceptual representations enabling us to distinguish an apple from a cherry; whereas the dorsal stream, in the occipito-parietal cortex, extracts the moment-to-moment visual information necessary to enabling us to open our hands wider to grasp the apple rather than the cherry. Seminal evidence of such a division of labour came from patient D.F. (Goodale, Milner, Jakobson, & Carey, 1991), a woman who suffered visual form agnosia following a lesion to her occipital-temporal cortex in the ventral stream (James, Culham, Humphrey, Milner, & Goodale, 2003) D.F. could not recognize objects by relying on the sole information of shape. For example, when given a series of rectangular blocks of different sizes, she performed very poorly as compared to when asked to discriminate these same blocks by reproducing their size using her finger and thumb with the distance recorded between them not varying accordingly with object size. Surprisingly, however, when she was asked to grasp the same objects using the same finger and thumb in a precision grip, their distance was proportional to the size of the objects (Goodale, et al., 1991)The fact that D.F. was able to use the shape of the blocks to guide her grasp, but not her perception, has been explained by suggesting: 1) that objects' visual processing for action and for perception engage separate brain pathways; and 2) the ventral stream in the occipito-temporal cortex, lesioned in D.F., guides vision for perception. A second patient, (R.V.) with a lesion in the parietal cortex (thus the dorsal stream) and suffering from Optic Ataxia (OA) was found to have the opposite problem. R.V. was very good at judging the size of the blocks, but she could not scale the opening of her fingers correctly when grasping (Jakobson, Archibald,

Carey, & Goodale, 1991), suggesting that 3) the dorsal stream is responsible for vision for action. Within this context, real and pantomimed actions have been used as an additional tool to tap into the visual transformations housed across the two visual streams. If it is true that the dorsal stream is tuned to the visual feature of objects for on-line actions (grasping and reaching), then it should not be involved in processing the same visual features when actions are not performed on-line and are instead guided off-line by internal representations (for example, when the actions are delayed or guided toward an object that is no longer present). When form agnostic patient D.F. and optic ataxia patient I.G. were asked to perform either immediate or delayed grasps toward objects of different sizes, the above predictions were fulfilled. While D.F. (with an impaired ventral stream and a spared dorsal stream) could scale the opening of her fingers to the size of the object for immediate on-line as compared to delayed grasps, patient I.G. (with an impaired dorsal stream and a spared ventral stream) performed in the opposite manner (by scaling her fingers to a better extent for the delayed as compared to the immediate grasp (Milner et al., 2001). D.F. was also tested in pantomime tasks in which she was asked to grasp imaginary objects of different sizes (Goodale, et al., 1994). In the delayed grasping task in which she needed to recall from memory, D.F. could scale her fingers according to the size of the object more precisely for the real as compared to the imaginary objects.

When D.F.'s age/sex matched controls were tested (Goodale, et al., 1994), it was found that their pantomimed reach-to-grasp actions were not identical to the real ones either. Indeed, it was found that pantomimed actions took longer to be performed, reached a lower peak velocity and described a higher wrist trajectory during the reaching phase. In addition, the distance between the index finger and thumb (grip aperture) was reduced overall and less precise during the approach phase. These results further suggest that real and pantomime actions represent different processes and in the intact brain. The advent of brain imaging further supported these initial observations. Functional MRI experiments measuring participants' brain activity while they performed real versus pantomimed actions (Kroliczak, Cavina-Pratesi, Goodman, & Culham, 2007) and immediate versus delayed actions (Singhal, Monaco, Kaufman, & Culham, 2013), thereby providing neurophysiological support for these same assertions. For both pantomimed and delayed actions, ventral areas located in the lateral Occipital Complex (delayed actions), right middle temporal gyrus and superior temporal sulcus were all recruited. In the real and in the immediate grasping actions, both studies reported activations in the dorsal stream. These results perfectly fit with other findings that

suggest that visual object processing takes place in the ventral stream (Cavina-Pratesi, Goodale, & Culham, 2007) and that object action processing for visually guided reaching and grasping instead activates the dorsal stream both within the Intraparietal Sulcus (IPS) and across both the posterior (Superior Parietal Occipital Cortex, SPOC) and anterior (aIPS) extent (Cavina-Pratesi et al., 2010). Collectively, both neuropsychological and imaging studied thus far have suggested that real and pantomimed actions are enabled via the recruitment of different brain circuits, and while performing real actions recruit areas in the dorsal stream, performing pantomimed actions recruits areas housed in the ventral visual stream.

Gender differences have captured the interest of cognitive scientists for very long time, and decades of research has documented dissimilarity in behavioural measures. It is quite accepted now that males perform better than females on spatial (Voyer, Voyer, & Bryden, 1995) and motor (Moreno-Briseno, Diaz, Campos-Romo, & Fernandez-Ruiz) tasks, while females perform better than males on some verbal and memory tasks (Hedges & Nowell, 1995) and measures of social cognition (Williams et al., 2009). More recently these difference have been replicated at the molecular (Jazin & Cahill, 2010), chemical, functional (Cosgrove, Mazure, & Staley, 2007), and connectivity (Jazin & Cahill, 2010) level. Despite a large body of behavioural and neuropsychological that have reported gender differences in certain praxis tasks, (Kimura, 1983, Chipman & Hampson, 2006) no studies to date has tested gender differences in real and pantomimed tasks. From previous evidence, we may expect that, within-hemispheric cortical processing along the posterior-anterior dimension involving the linking of perception to action, would confer an efficient system for more efficient visuomotor actions in males. We note that neuropsychological data also indicates that females with damage to their left frontal cortex are much more likely to be diagnosed with manual apraxia (Kimura, 1983) compared to females with damage restricted to more posterior areas of their left parietal cortex. Males, on the other hand, are just as likely to show apraxia after lesions to either anterior (frontal) or posterior (parietal) areas. Moreover, females have been shown to be better than males at manual praxis tasks requiring rapid selection amongst different unrelated sequential hand movements (Chipman & Hampson, 2006). These data suggest that the cortical networks underlying manual praxis abilities may indeed differ between men and women. Furthermore, given that men have been found to rely less on the praxis system when other sensory cues are available (for example visual ones) (Chipman, Hampson, & Kimura, 2002), the presence of visual feedback could also be

relevant in recording any possible gender differences. Indeed, while comparisons between real and pantomimed grasping actions have been tested in both male (Cavina-Pratesi, Kuhn, Ietswaart, & Milner) and female (Goodale, et al., 1994) participants separately (and in both cases the classic kinematic differences between the two types of grasps have been reported), experiments performed with males were performed in so-called open loop only (Cavina-Pratesi, et al.) and studies performed in females were mostly performed under close loop conditions (with visual feedback present).

In the present study we asked male and female participants to perform reach-to-grasp actions toward real and imagined objects using either their right or left hand. Grasping actions could be performed either with or without visual feedback, hereby described as closed loop (with visual feedback) and open loop (without visual feedback). It is worth underlining that the present research focuses on grasping actions using a precision grip in which the thumb and index finger are used to pick up or use a small object (Castiello, 2005). Motion Analyses of precision grips have revealed that reach-to-grasp actions rely on a very specific motor sequence that begins much earlier in time than the actual contact with the object. In a standard precision grasp, the fingers begin to scale according to the shape and size of the object during the approach phase. After reaching a maximum opening (usually referred as Maximum Grip aperture or MGA), the fingers tend to close until they match the size of object that is to be grasped (here referred as Contact Grip Aperture, CGA). During the approach phase other parameters such as the amplitude (Movement amplitude, MA) and the velocity (Peak Velocity, PV) reached by the wrist, and the time the hand takes from the moment it moves to the moment it contacts the object (Movement Time MT) will be recorded. Male and female performance will be compared by analysing the above key kinematic markers.

2. Methods

2.1 Participants

A total of 20 participants, with an age range of 22-47 (mean age 25.3; women: 27.4 year, men: 23.6 ($t_{(9)}$ = 1.376, p = 0.199) were recruited from staff and students of the University of Durham. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), with a mean Laterality Quotient (LQ) of 96.5 (women: 100; men: 92.9 ($t_{(9)}$ = 1.843, p = 0.099). Participants with pre-existing motor control deficits of any

etiology were not accepted, nor were participants with any condition that could be exacerbated by repetitive movement generation (arthritis, RSI etc.). The present experiment was approved by the Ethics Committee of the Psychology Department at the University of Durham.

2.2 Apparatus

Kinematic data was recorded using a miniBIRD model 800 magnetic tracking system (Ascension Technology Corporation, Burlington, VT, United States of America). Three sensors with dimensions of 8.1mm x 8.1mm x 18.1mm were used and these recorded at 86Hz for four seconds per trial. When measuring the right hand, the first two sensors were placed in line with the right edge of the thumbnail and the left edge of the index fingernail, and the third placed on the left side of the wrist, opposite the styloid process. When measuring the left hand this was inverted to place the first two sensors in line with the left edge of the thumbnail and the right edge of the index fingernail, with the third sensor located on the right side of the wrist.

As shown in **Figure 1**, Participants were presented with a working space of uniform appearance, black in colour and 60cm x 42cm in area. The objects presented were grey plastic Efron Shapes, varying in shape and thus in grip aperture demands, but identical in overall surface area; they were a thin rectangle (2.5 x 10 x 1cm); a wide rectangle (4 x 6.25 x 1cm) and a square (5 x 5 x 1cm). The first dimension listed is that along the axis of the reaching movement. The non-linear increment in size assured us that the pantomimed actions could not be programmed toward conceptual size of small, medium, and large objects. Area-matched, angled objects were used rather than cylinders to prevent confounds arising from perceptual differences in overall size (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994).

Please, include figure 1 here

The placement of the objects within the experimental workspace varied with the test condition. During real movement trials (**Figure 1a**), the object was placed with its nearest edge 30 cm away from the starting position, in the centre of the workspace. During pantomime trials (**Figure 1b**), the object to be pantomimed was displaced 8cm to the

opposite side from the participant's hand (i.e. 8 cm toward the left or to the right accordingly to whether the participants were using their right or left hand, respectively), to prevent it acting as a perceived obstacle along the reach-to-grasp trajectory. Despite this displacement, the pantomime action was still targeted directly ahead of the participant, as if the imaginary object were placed in a matching position to the objects during the real movement trials. This arrangement ensured that the basic motor mechanisms of the reach-to-grasp actions were held constant for real and pantomimed actions.

To control visual feedback, PLATO visual occlusion goggles (Translucent Technologies Inc., Toronto, Canada) were used. The lenses of the goggles vary from an 'open' condition of clear glass to an 'opaque' condition in which vision is occluded, but with the overall light level being entirely preserved (thereby eliminating confounds arising from adaptation to light).

2.3 Procedure

The experiment was designed to test participants on all possible combinations of object size (small (S), medium (M) or large (L)); hand used (Right or Left); visual feedback (closed loop) or (open loop)) and grasp type (Real or Pantomimed). Each participant was tested in seven trials per size/hand/feedback/grasp combination, totalling 168 trials per participant.

Participants began each trial holding down a start button (starting position) with their thumb and index finger, while wearing the occlusion goggles in their opaque setting. In each trial, the goggles opened and remained open for 1000ms, at which point a tone sounded to signal movement onset. In the closed loop condition, the goggles remained open for the next 3000 ms and closed again at the end of the trial. In the open loop condition, once the start button was released at movement onset, the goggles rapidly transitioned to opaque and remained so throughout the trial.

During the Real grasp trials, participants were required to reach directly toward the object, grasp the object in a precision grip using the index finger and thumb in line with the axis of movement, lift it, and placing it at about 8 cm either to the left (for right hand movements) or to the right (for left hand movements) on a specific red target spot prior to returning to the start button. In the Pantomimed grasp trials, participants were required to make movements as if an object identical to the one presented either in their right (for left

hand movements) or left space (for right hand movements) were directly ahead of them, by grasping it, lifting it, by placing it on the target spot, and again returning to the start button at the end of the movement.

Target objects were positioned by the experimenter and on a trial-by-trial basis. The order in which the objects were presented was randomised, and the combinations of conditions (real grasp open loop, real grasp closed loop, pantomimed grasp open loop, pantomimed grasp closed loop) were presented in a counterbalanced order across the participants. At the beginning of the block, the participant was informed which combination of conditions was to be expected, to access the exaggeration of kinematic effects which reliability of circumstance in blocked trials produces (Whitwell & Goodale, 2009). Left and right hand grasping tasks were also presented in different blocks. Half of the participants in each gender group were tested with their right hand first; the other half with their left hand first.

2.4 Data Analysis

Analyses were performed on reaction time (RT) and on traditional components of the transport and the grip phases. For the transport phase we collected movement time (MT), peak velocity (PV), time to peak velocity (TPV) and wrist movement height). For the grip phase we collected maximum grip aperture (MGA) and time to maximum grip aperture (TMGA). Data analysis was performed on the proximal (reaching) component and the distal (grip) component of the reach-to-grasp actions separately. RT was measured as the time interval between the auditory start signal and movement onset (defined as the time at which the velocity of the wrist marker exceeded 50 mm/s). MT was measured as the time between movement onset and movement offset, which was defined as the time when the velocity of the wrist marker became less than 50 mm/s. Wrist height was calculated as the displacement of the wrist marker on the z dimension from the table. PV was defined as the maximum resultant velocity of the wrist marker within the time of the outward movements. MGA was computed as the maximum distance in 3D space between thumb and index markers during the outward hand movement. TMGA was computed as the time interval between movement onset and MGA. We computed one additional variable for the grip component analysis: grip overshoot. ''Grip overshoot'' was computed as the difference in mm between MGA and the contact grip aperture (CGA), which was measured as the distance between the index finger and thumb markers while holding for real or pretending to hold for pantomimed actions the

object at the end of the reaching phase. Data points just before object lifting (i.e. before speed of the thumb marker rose again above 50 mm/s after landing at the object and before lifting it) were chosen as the clearest contact grip aperture landmark for both the real and the pantomimed grasps. In addition, in order to test the precision with which participants shaped their hands, we computed the scaling precision for both MGA and CGA. To do so, R^2 values resulting from the linear regression between MGA/CGA and object size were computed for each participant and for each condition separately. The data were analysed using a mixed repeated-measures ANOVA where GRASP (real, pantomimed), VISION (open and closed loop), HAND (left and right hand) and SIZE (S, M, L) were used as within-subjects factors. GROUP (male and female) was used as a between-subjects factor. The ANOVA used to compare R^2 values was computed without the within-subjects factor SIZE. Due to recording artefacts or other technical difficulties, 40 trials (1.2%) were rejected across all of the participants that were tested.

3. Results

Given the richness in kinematic-dependent variables and given that our goal was to identify any possible difference between real and pantomimed actions across genders, our analysis will focus on those results that include a GRASP x GROUP interaction.

3.1 Interactions including GRASP x GROUP

Confirming previous results, we found that pantomimed grasps showed a smaller peak velocity, a larger movement amplitude and a smaller grip aperture. Indeed, lower PV ($F_{(1,18)}$=20.25, p=0.0001), higher wrist height ($F_{(1,18)}$=60.8, p=0.0001), and smaller MGA ($F_{(1,18)}$=15.04, p=0.001). Critically, we found a group by task interaction in some of the parameters suggesting that indeed real and pantomimed tasks differed across gender. A GRASP x VISION x GROUP interaction was found whereby PV ($F_{(1,18)}$=4.89, p=0.04),wrist height ($F_{(1,18)}$=8.04, p=0.011), and MGA ($F_{(1,18)}$=6.03, p=0.024) did not differ for Real and Pantomimed grasps in closed loop conditions for male, but not female participants. This was assessed by the use of two separate repeated measures ANOVAs, using GRASP (real, pantomimed), VISION (open and closed loop), HAND (left and right hand) and SIZE (S, M, and L) run separately for male and female participants for each dependent variable. As expected, the interaction GRASP x VISION was significant in male (PV= $F_{(1,9)}$=5.93, p=0.039; wrist height = $F_{(1,9)}$ =10, p= 0.012; MGA = $F_{(1,9)}$=26.53, p=0.001) but not in female participants (PV = $F_{(1,9)}$=2.96, p=0.118,wrist height = $F_{(1,9)}$=0.132, p=0.75; MGA = ($F_{(1,9)}$=2.85, p=0.13). As shown in **Figure 2**, when male participants could see both their own hand and the work space (clear background in the graphs) the velocity of their movements (Pantomimed = 864 mm/sec; Real = 876 mm/sec, $t_{(9)}$=1.6, p=0.14), the amplitude of their reaches (Pantomimed = 91.8 mm, Real = 88.7 mm, $t_{(9)}$=-1.3, p=0.22) and the aperture of their hand (Pantomimed = 74.9 mm, Real = 75.1 mm, $t_{(9)}$=-0.3, p=97) failed to reach significance for both real and pantomimed actions. Conversely, when operating in open loop (i.e. without vision of the hand and the working space, grey background in the graphs), male participants showed the standard pattern of results with lower peak velocity (Pantomimed = 770 mm/sec; Real = 830 mm/sec, $t_{(9)}$=4.5, p=0.001), higher wrist height (Pantomimed = 103 mm, Real = 85.7 mm, $t_{(9)}$=3.84, p=0.004), and smaller MGA (Pantomimed = 70.7 mm, Real = 85.1 mm, t(9)=-5.2, p=0.001) for pantomimed as compared to real grasps. Female participants instead showed lower peak velocity (Pantomimed =821 mm/sec; Real = 879 mm/sec, ($F_{(1,9)}$=9.7, p=0.012), larger wrist height (Pantomimed = 102.8 mm, Real = 87.3, $F_{(1,9)}$=83.4, p=0.0001),

and smaller MGA (Pantomimed = 72.9 mm, Real = 80.3 mm, $F_{(1,9)}$=7.9, p=0.020) for pantomimed as compared to real grasps regardless of the visual condition. Inspection of **Figure 2a**, **b**, and **c** reveals that in closed loop conditions male participants performed pantomimed grasp as they were real grasps for all variables. Pantomimed actions in closed loop showed significant differences to pantomimed actions in open loop: they showed a higher PV ($F_{(1,9)}$=-7, p= 0.0001); a lower wrist height ($F_{(1,9)}$=-4.4, p=0.002); and larger MGA ($F_{(1,9)}$=-3.1, 0.012). A GRASP x GROUP interaction is reported for the grip overshoot also ($F_{(1,9)}$=6.38, =0.021)). Inspection of **figure 2d** suggests that while grip overshoot was larger for real as compared to pantomimed grasps in females regardless of visual conditions, male participants overshot similarly for real and pantomimed actions in closed loop conditions only. This was assessed by the use of two separate repeated measure ANOVAs using GRASP (real, pantomimed), VISION (open and closed loop), HAND (left and right hand) and SIZE (S, M, and L), run separately for male and female participants. A VISION x GRASP interaction was found for male participants ($F_{(1,9)}$=14.65, p=0.004)), but not for females ($F_{(1,9)}$=0.037, p=85)). Crucially, post hoc t-tests for male participants showed that grip overshoot was higher for Real grasps as compared to Pantomimed grasps in open loop ($t_{(9)}$=-3.5, p=0.007) but not in closed loop conditions ($t_{(9)}$=-0.18, p=0.86).

Please, include figure 2 here

3.2 Dependent variables not showing a GRASP x GROUP interaction

None of the other variables resulted in a GROUP x GRASP interaction. RTs were similar across GROUPS ($F_{(1,18)}$=0.658, p= 4.28). We found significant main effects for GRASP ($F_{(1,18)}$=105.9, p=0.0001), and VISION ($F_{(1,18)}$=8.35, p=0.010) reflecting faster responses for Real (472 ms) as compared to Pantomimed (802.3 ms) grasps and for closed loop (620.4 ms) as compared to open loop (654 ms) conditions. The remaining main effects or any of interactions failed to reach significance. MT did not differ across GROUPS ($F_{(1,18)}$=3.6, p= 0.073)) with males and females taking an equal time to contact the objects (females = 723.3 ms, males = 856.1 ms). Significant results were found for the main effects for Stimuli ($F_{(1,18)}$=8.1, p=0.001) and Hand ($F_{(1,18)}$=2.9, p=0.025). It took participants longer time to contact the small object (818.7 ms) compared to the medium (816.3 ms, $t_{(9)}$=-3.312, p=0.012) and the large (793.7 ms, $t_{(9)}$=-3.26, p=0.013) ones, which in turn did not differ from each other (t(9)=0.41, p=0.97). In addition, movements made with the left hand (788.5 ms) resulted in faster MT as compared to the ones executed with right hand (830.8 ms).

Interestingly, we recorded a GRASP x HAND interaction reporting an increase in MT with the left hand were made for the Real ($t_{(9)}$=2.68, p=0.015, but not for the Pantomimed grasps. TPV did not reach significance for the main effect of GROUP (f(1,8)=2.7, p=0.115)), but it was longer for grasps executed in open loop (VISION, $F_{(1,8)}$=5.32, p=0.33; closed loop = 328.4 ms, open loop = 342.9 ms)) and for pantomimed as compared to real grasps (GRASP, $F_{(1,8)}$= 13, p=0.002, Real = 326.5 ms, Pantomimed = 344.7 ms). None of the interactions reached significance. TMGA was similar across GROUPS ($F_{(1,18)}$=1.11, p=0.3)). Significant main effects were found for VISION ($F_{(1,8)}$=17.4, p=0.001), HAND ($F_{(1,18)}$=6.6, p=0.019], and STIMULI ($F_{(1,18)}$=35.1, p=0.0001) with longer TMGA recorded for Real (563.4 ms) as compared to Pantomimed (551.9 ms) grasps, for Right (579.1 ms) as compared to Left (536.2 ms) hand, and for large (590 ms) as compared to medium (567.7 ms) and small (515.3 ms) stimuli (for all comparisons, p<0.002). None of the interactions reached significance. Analyses of hand scaling PRECISION for MGA showed a main effect of VISION ($F_{(1,18)}$=13.6, p=0.002), reflecting higher precision for grasping actions performed in closed loop (R^2= 6.72) as compared to open loop (R^2=5.9); and a main effect of GRASP ($F_{(1,18)}$=18.4, p=0.001) showing higher precision for real (R^2= 0.687) as compared to pantomimed (R^2= 0.595) grasps. Analyses of hand scaling precision for CGA showed a main effect of HAND ($F_{(1,18)}$=7.5, p=0.013), reflecting higher precision for grasping actions performed with the right (R^2= 0.766) as compared to the left (R^2=0.724) hand. In addition, as shown for MGA, we recorded and a main effect of GRASP ($F_{(1,18)}$=8.23, p=0.01) showing higher precision for real (R^2= 0.813) as compared to pantomimed (R^2= 0.737) grasps. The lack of GROUP x GRASP interaction for the precision of both MGA and GC is crucial as it shows that kinematic differences for real and pantomimed grasps between genders found for the MGA values are not due to a decline in the overall precision of the performance. MGA variability was computed in order to gain insight as to whether the GROUP x TASK interaction found for the MGA values was due to different degrees of uncertainty between the two groups. We reasoned that the higher the uncertainty, the higher the MGA variability. A repeated measure ANOVA showed that the only difference recorded in MGA variability was the main effect of GRASP ($F_{(1,18)}$=23.82, p=0.0001) with larger variability for pantomimed (66.3 mm) as compared to real (32.01 mm) grasps.

3.3 Practice effects

In order to test whether or not the differences between the two groups built through the testing sessions we divided each participant dataset into first and second halves of the trials and ran several repeated measures ANOVAs for PV, wrist height, MGA and grip overshoot using GRASP (real, pantomimed), VISION (open and closed loop), HAND (left and right hand), SIZE (S, M, and L), and SESSION (first half and second half) as within subject factors and GROUP (male and female) as the between subject factor. Trials were aligned accordingly to the order of presentation and divided into two equal halves. The interaction TASK x VISION x GROUP x SESSION was not significant for PV ($F_{(1,8)}=0.009$, p=0.92),wrist height ($F_{(1,8)}=1.4$, p=0.25), MGA ($F_{(1,8)}=0.3$, p=0.58), and grip overshoot ($F_{(1,8)}=1.6$, p=0.22), suggesting that the differences recorded between groups were not due to any learning strategies put in place through the testing session. Of interest here is the finding that a main effect of SESSION was recorded for MGA ($F_{(1,8)}=14.9$, p=0.001) and for grip overshoot ($F_{(1,8)}=6.7$, p=0.018). While MGA was higher in the first half of the session (first half = 75.6 mm, second half = 74.2 mm), grip overshoot was found to be larger in the second half (first half = 17.4 mm, second half = 18.2 mm).

4. Discussion

Here we report results that demonstrate gender differences in performing pantomime tasks in which male and female participants were asked to perform a reach-to-grasp action toward an imaginary object situated in front of them. Such imaginary objects should have been identical in shape and size to a 3D object positioned slightly offset to the left or right side of their own peripersonal space. Real and pantomimed actions were executed under two different visual conditions: with and without visual feedback (closed versus open loop). Interestingly, gender differences were found for pantomimed actions, and only in the presence of visual feedback. The gender difference we recorded had to do with the fact that male participants performed pantomimed actions that were not distinguishable from the real ones. Indeed, most of the kinematics parameters we collected (MT, PV, TPV, MGA, TMGA) were similar for real and pantomimed tasks in males when vision of the working space was available. Conversely, females recorded substantial differences between the real and the pantomimed reach-to-grasp actions in both visual conditions. Indeed, their reach was slower and wider in amplitude and their grip was overall smaller on object approach. Seen from a naïve observer, females would approach the object slowly and by performing a high arch with their arms. In addition, their hands would open without closing around the imaginary object upon pick-up. This particularly "peculiar" behaviour is not surprising as the imaginary object does not require overshooting necessary to put in place a more stable grasp to lift the object. Nevertheless, this being stated, the males pantomimed toward the imagined object overshooting on object approach as if the real one was, in fact, present. In other words, it can be argued that the males were much better at faking actions than females. The fact that differences between genders under visual feedback were recorded for all the kinematic parameters makes us confident that participants did not try to consciously ameliorate any specific aspects of the actions, but rather, all participants treated the pantomimed movements as an almost ecological movement. In addition, by dividing our trials into first and second halves, we were then able to rule out the possibility that gender differences could be simply attributed to practice effects.

Our findings regarding MGA and peak velocity from the female participant group matches those of experiment three in Goodale and co-workers (1994). The trial-structure of the present experiment largely replicated this earlier one, and the Goodale study participant pool was drawn from an entirely female participant group. Studies which did not specify the

gender balance of participants have also produced results that match the present ones. For example, Zahariev & MacKenzie (2007) reported that MGA was increased for real as compared to virtual objects, with a decrease in MGA when augmented feedback was removed. Based on the above pattern or results of this earlier experiment, our results suggest their participant group would likely have been entirely or in the majority female. Other studies examining visual feedback or pantomime and real gesture in grasping do not entirely accord with the present findings. Whereas certain studies produce differing results which may be attributed to gender imbalance in sample or other factors, others have shown the same behavioural patterns as we observed while using mixed-gender groups (Westwood, McEachern, & Roy, 2001; (Fukui & Inui, 2013; Whitwell, Lambert, & Goodale, 2008).

Studies involving manipulation of visual feedback have often reported opposing results to the findings of the present study, which may be attributed to the absence of controls for gender in sampling. For example, (Westwood, McEachern, & Roy, 2001) were primarily concerned with delay effects on reaching: however, their 'full vision' and 'open-loop' conditions closely match our real grasp conditions both with and without visual feedback, respectively, lending validity to a comparison of the results obtained regarding peak velocity. They reported no difference in peak velocity attained and this is linked to the presence or absence of visual feedback during reaching. As their participant group was mixed-gender, consisting of 6 men and 4 women, it is highly likely that this absence of an effect is owing to a confound of gender, and raises questions about whether or not similar confounds may have disrupted their conclusions regarding delay effect(s) also. Other studies with mixed-gender participant groups have reported the same absence of effect on peak velocity, while still showing larger MGA in the absence of visual feedback (Fukui & Inui, 2013; Whitwell, Lambert, & Goodale, 2008).

Studies of pantomime movement by contrast tend to show results that provide support for the present findings, but with mixed-gender groups. For example, Mason and co-workers (2001) reported the same effect we identified for MGA using a group of males and females; in their study, however, the group was particularly small in sample size, with only 3 female and 2 male participants, and we therefore must consider statistical issues that may arise as underlying the apparent absence of a gender effect. It is particularly of interest that they report, in examining the eigenposture identified with MGA in E2, that their subjects divided 3:2 in some of the kinematic characteristics of grip closure. By choice of pronouns and

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descriptions of relative hand size elsewhere in the study, it becomes evident that at least one and possibly two of the participants in that majority group were female. We suspect that this methodology, reproduced with a larger sample size, could be shown to produce effects of gender that would be highly consistent with the present findings. Westwood and co-workers (2002) examined grasping toward 2D and 3D targets, which they considered an effect consistent with the task being treated in the same manner as pantomime by the visuomotor system. The task was performed with visual feedback throughout movement, and they report finding evidence for a larger MGA in grasping 3D objects than 2Ds ones in three of their five participants. The gender balance of their study was 3 female to 2 males. These results make us confident that in this case, their findings and ours were consistent – merely unexamined in terms of a gender interaction. A more recent publication (Fukui and Inui, 2013), in which six males and one female were asked to perform real and pantomime tasks with and without visual feedback, reported that MGA for real and pantomimed actions were similar for most eccentricities only when visual feedback was available, supporting our results.

The main point to discuss now will focus on why male and female participants differ in performing pantomime tasks. The present data show that when visual feedback is available males perform pantomime grasping task as if it were real grasping tasks. This further infers that their improvement must be the result of seeing the real object, their own hands, or both.

In a previous study we reported that as compared to a group of age and gender matched controls, male magicians could perform pantomime tasks toward an imagined object situated beside the real one as if they were performing grasps toward real objects when vision was not available (Cavina-Pratesi, et al.). Furthermore, unpublished data from our laboratory showed that just as in the present case, the performance of magicians and gender/age matched controls did not differ when vision was available – when both groups had the possibility to see the workspace, MGA for real and pantomimed tasks did not differ. This raises the question of how visual feedback of the object and/or the hand improves performance in males but not in females. It is worthwhile to note that in western society professional male magicians outnumber their female counterparts (Webster, 1948). In our study we advanced the hypothesis that magicians could perform pantomimed grasps as well as real ones because they might use the visual information coming from the real object while planning the reach-to-grasp action toward a different nearby location (i.e. the location where the imagined object should be located).   Given that no specific instructions were given to the participants

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regarding where to look, we are tempted to put forward the hypothesis that magicians during both open and closed loop (and control male participants in close loop only) gathered the visual information necessary to perform the pantomime action from the real object by gazing at it explicitly. This could also explain why both groups failed to record similar MGA for real and pantomimed actions in a second experiment, in which the real objects were not present at all and their reach-to-grasp actions were directed toward an imagined object only. In such case the actions needed to be executed toward an internal representation and, as a consequence, significantly different kinematic measurements were reported for real and pantomimed actions. To substantiate our speculations, we have carried out a substantial control experiment in which a new set of self-declared right handed participants (8 males, mean age 23.6 years old) and 8 females, mean age 24.3years old) were asked to perform real and pantomimed actions with the difference that no real object was presented in the pantomimed condition) (i.e. pantomimed grasps were performed using the sole imagining abilities of the individuals. The experiment was run following the specific procedures described in Cavina-Pratesi et al. 2011, Experiment 2, in which participants either grasped real batteries of different sizes (AA, C, D) or pretended to grasp imagined batteries of the same size (the size of the battery was written in a piece of paper in front of the participant on a trial by trial basis to instructs the size of the pantomimed grasp). Real and pantomimed grasps where run in separate blocks. Our results in figure 3 clearly support the idea that under these circumstances, the different pantomiming abilities of males and female disappeared. Indeed, for both male and female participants (GROUP ($F_{(1,14)}$=222.5, p=.57) MGA was larger for real (67.8 mm) as compare to pantomimed (64.8 mm) grasps ($F_{(1,14)}$=101.6, p<0.0001), and as a function of the battery's sizes (small for A, medium for C and larger for D; for all comparisons, p=0.001, see figure 3). The impact of the presence versus the absence of a real object in grasping tasks is supported by several sources of indirect evidence. Firstly, fMRI data have shown that grasping area aIPS in the anterior portion of the posterior parietal cortex (thought to transform the visual information of the object into the correct hand shape for grasping) is activated only when grasping actions are elicited by real three dimensional objects (Cavina-Pratesi, et al., 2007) as compared to imagined ones (Kroliczak, et al., 2007), or 2D images (Culham et al., 2003). The second line of support is based upon an fMRI study investigating gender difference in tasks in which participants were asked to perform visually guided actions toward spatial locations that did and did not correspond to the position of the target: pro- and anti- pointing and pro- and anti-saccade tasks (Gorbet & Sergio, 2007). In anti-pointing and in anti-saccade tasks the mapping between a given visual cue and the

response that it guides is considered non-standard (Wise, di Pellegrino, & Boussaoud, 1996) and it is in direct contrast to the so called standard mapping where the spatial position of the cue corresponds to the location of the corresponding action. Despite no gender difference in behavioural accuracy being reported in standard and non-standard mapping tasks, fMRI data showed gender differences in the pattern of brain activity mostly associated to the type of mapping used. Specifically, the standard mapping tasks (pro-saccade and pro-pointing) showed different degrees of activation for males and females in motor, somatosensory, premotor and parietal regions. Areas in the insular cortex and in the lateral temporal cortex were instead found to be different for the non-standard mapping (anti-saccade and anti-pointing). Critically, these same areas are often reported to become active during multisensory integration (Downar, Crawley, Mikulis, & Davis, 2000), particularly when the visual and somatosensory information sources are not congruent (Balslev, Nielsen, Paulson, & Law, 2005). Perhaps gender differences found in lateral temporal cortices are due to differences in processing visual cues when the information guiding the arm is spatially dissociated from the executing effector, and therefore from the somatosensory feedbacks (Gorbet & Sergio, 2007). This would also fit with fMRI data which demonstrate that experiments comparing real versus pantomimed reaching and grasping actions toward imagined objects reported pantomime-related activity in the right temporal cortices. Although these results need to be evaluated carefully, given that a balanced number of male and female participants were examined, neuropsychological studies in patients with unilateral neglect and lesions that include the lateral temporal cortices showed different impairments for male and female participants when performing anti-pointing tasks (Rossit et al., 2011). Although not specifically addressed in the text, landing errors for anti-pointing tasks (reported in millimetres in Table 2) were significantly larger (p=0.047) for females (14.2 mm) as compared to males (7.6 mm). This difference could not be accounted for factors such as age (p=0.19), time from lesion onset (p=0.28), or lesion size (p=0.23). The latter results clearly demonstrate gender differences in non-standard (or off-line) visually guided action (with females underperforming compared to males) following a lesion involving the temporal cortex (which was found to be crucial for the difference between pantomimed as compared to real actions, and in gender difference for non-standard mapping tasks in fMRI experiments (Gorbet & Sergio, 2007).

We now return to the present results. Here we put forward the hypothesis that when visual feedback is available male participants perform their grasping action by dissociating

the location of the targeted object from the location toward which they perform the actual action (as in a non-standard mapping task). While looking directly at the real visual object, male participants might direct their hand toward the nearby location. Female participants on the other hand might not do the same and instead gaze toward the same imaginary location toward which they are moving their hand. Looking away from the target of the ongoing action is a typical trick performed by magicians (Kuhn, Amlani, & Rensink, 2008)and it could then be possible, given the low number of female magicians) that males find less difficulty than females in looking in one direction and acting toward a different one. The lack of gender differences recorded when the real object is not present for pantomiming suggests that different gazing strategies might actually be the key issue. The exact cognitive mechanisms that allow males to outperform females in disentangling gaze direction and overt action is still not clear. We suspect that well known gender differences on spatial abilities such as mental rotation ((Kail, Carter, & Pellegrino, 1979); (Tapley & Bryden, 1977) may play a role.

To be comprehensive, it should be noted that gender differences in pantomimed tasks have not been found in studies investigating tool use (Hermsdorfer, et al., 2012; Laimgruber, et al., 2005). Indeed, the scoring received by participants performing pantomimed actions such as hammering or scooping was similar for males and females. This discrepancy might rise because pantomiming the use of a hammer or a spoon (particularly when the context is not present) does not require non-standard mapping, which may be the key aspect leading to gender differences in our study and those discussed above. In addition, as reported by Laszio et al. (1980), it could also be the case that when visual feedback is present, female participants perceive the real object more like a distractor as compare to a facilitator, and this is why their performance is not as robust as males who instead make the real object the visual cue of their actions.

4.1 Conclusions

The present experimental results have implications for neuropsychology and for theories of vision. The observation that males and females recorded significant differences in behavioural tests (Rossit et al., 2011) and in brain imaging studies (Bell, Willson, Wilman, Dave, & Silverstone, 2006; Gorbet & Sergio, 2007) suggest that male and female patients should be evaluated separately in the clinical environment, and should be reported and analysed distinctly in future research. Non-standard mapping tasks such as anti-saccade tasks

are currently used as markers of neurologic (Alzheimer's, Huntington's, Lateral Sclerosis, Parkinson's), psychiatric (Schizophrenia), and developmental (Autistic Spectrum) disorders (Everling, Dorris, & Munoz, 1998; Luna, Velanova, & Geier, 2008). As such, subdividing participants according to gender might clarify discrepancies in the literature regarding these conditions (Everling, et al., 1998; Hutton & Ettinger, 2006), and has the potential to improve both diagnosis and the evaluation of treatment in future clinical trials. As for theories of vision, the present data provide further support for the idea that vision for action in standard mapping task is not (or is only moderately) affected by gender differences. Nevertheless, as predicted by Goodale and Milner (Milner & Goodale, 1995), when actions are guided by the ventral visual stream, cognitive differences then arise and change the behaviour and brain activities across males and females. It follows then that studies investigating off-line (or non-standard mapping) actions should seek to collect, analyse, and report their data separately by participant gender.

From a relatively wide-ranging standpoint, the notion that genders differ in non-standard, off-line tasks is relevant in current times, where everyday interactions with new technologies such as a computer mouse, computer keyboards, and trackpads expose us to such non-standard mapping actions constantly. We emphasise, however, that the present data should not crystallize the idea that female participants cannot perform non-standard mapping tasks. Elsewhere, preliminary data from our laboratory showed that female Indian dancers, who are trained in various forms of mime, performed pantomimed grasping actions more precisely than a group of age and gender control participants. For example, the grip aperture of the Indian dancers better approximated the size of the real objects they were asked to pantomime, suggesting that practice (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008) could indeed counteract strategic, structural and functional differences in task performance.

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Figures captions

Figure 1. Schematic representations of a participant hand performing Real (a) and Pantomimed (b) grasping tasks. While in the real grasping tasks, participants performed movements toward a visible real object (depicted in continuous lines and filled in grey), in the pantomimed grasping tasks participants performed movements toward an imagined object (depicted in dotted lines and filled in white) identical to the real one and located just beside it. In both tasks, the participants' hand started from a common starting position so that the grasping movements could be performed using a straight ahead movement. The image also depicts the position of the thumb, index finger and wrist markers.

Figure 2. Variables showing an interaction with the factor GROUP. (a) Peak Velocity (PV), (b) wrist height, (c) Maximum Grip Aperture (MGA) and (d) Grip Overshoot. For each variable, mean and standard errors for real (in white) and pantomimed (in grey) grasps are plotted separately for Females (on the right hand side) and Males (in the left hand side) groups and for open loop (grey background) and closed loop (white background) conditions. MGA aperture data has been plotted against stimulus size for clarity purposes although the factor SIZE did not contribute to the interaction. Asterisks represent significant differences between real and pantomimed grasping tasks.

Figure 3. MGA is plotted as a function of real (white) and pantomimed (grey) grasping actions for a control experiment. The pantomime condition is named "absent" as no real object was presented. While in the real grasping task participants grasped batteries of various sized (AA <, C < D), in the pantomimed grasping tasks, participants were presented with the name of the battery and ask to imagining it in order to pretend to pick it up. Asterisks represent significant differences between real and pantomimed grasping tasks. Crucially, we did not record any gender difference.

Figure 1
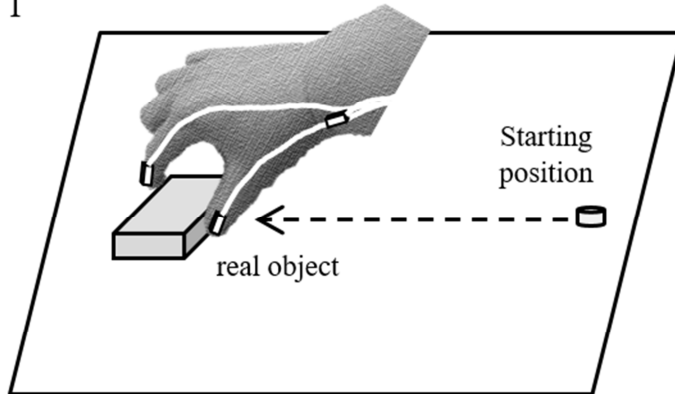
a. Real Grasp
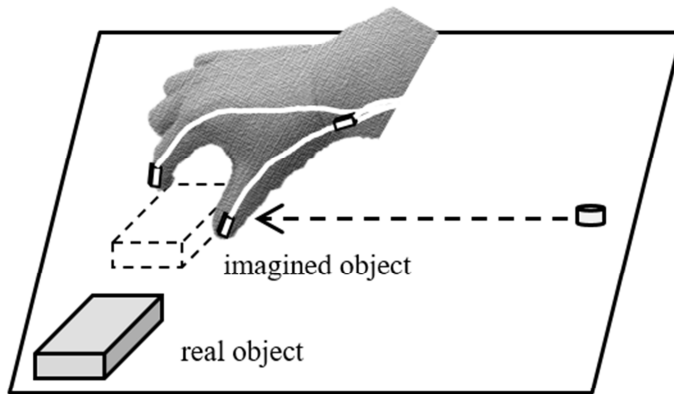
b. Pantomimed Grasp

Figure 2

☐ Real ◼ Pantomimed