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Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: A TMS approach

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ABSTRACT

According to Milner and Goodale's theory of the two visual streams, the dorsal (action) stream controls actions in real-time, whereas the ventral (perceptual) stream stores longer-term information for object identification. By this account, the dorsal stream subserves actions carried out immediately. However, when a delay is required before the response, the ventral (perceptual) stream is recruited. Indeed, a neuroimaging study from our lab has found reactivation of an area within the ventral stream, the lateral occipital (LO) cortex, at the time of action even when no visual stimulus was present. To tease apart the contribution of specific areas within the dorsal and ventral streams to the online control of grasping under immediate and delayed conditions, we used transcranial magnetic stimulation (TMS) to the anterior intraparietal sulcus (aIPS) and to LO. We show that while TMS to aIPS affected grasp under both immediate and delayed conditions, TMS to LO influenced grasp only under delayed movement conditions. The effects of TMS were restricted to early movement kinematics (i.e. within 300 ms) due to the transient nature of TMS, which was always delivered simultaneous with movement onset. We discuss the implications of our findings in relation to interactions between the dorsal and ventral streams.

1. Introduction

Since 1992 Milner and Goodale have proposed and refined a highly influential theory that two cortical visual streams, the ventral and dorsal stream, separately subserve perception-for-vision and perception-for-action, respectively (for reviews, see Goodale & Milner, 1992; Milner & Goodale, 1995, 2006, 2008). In addition, they argued that these two visual streams operate on different time scales. The ventral stream, projecting from striate cortex to infero-temporal cortex, represents an object over time, allowing object characteristics to be maintained and thereby aiding object recognition across different viewing conditions. The dorsal stream, projecting from striate cortex to posterior parietal cortex, mediates actions towards targets that are likely to continuously change, and therefore it works in real-time for immediate use in guiding actions.

Evidence to support this theory has been seen in patients with visual form agnosia and optic ataxia. Patients with damage to structures in the ventral stream may develop visual form agnosia, demonstrating profound problems with object recognition through vision. In particular, visual form agnosic patient D.F. shows movement errors if a delay is introduced between the visual stimulus and motor response (Goodale, Jakobson, & Keillor, 1994; Milner, Dijkerman, & Carey, 1999), but she shows intact performance on tasks requiring immediate action (Goodale, Meenan, et al., 1994; Rice, McIntosh, et al., 2006). Although most of the published evidence for this finding comes from a single patient, D.F., these results have now been replicated in a second patient, M.C., with impaired object recognition despite intact motion detection (Goodale et al., 2008). In contrast, damage to structures in dorsal stream regions may lead to optic ataxia, characterized by the opposite pattern of impairment; that is, they show intact performance when a delay is introduced between the stimulus and response and impoverished performance when the response immediately follows the stimulus (Goodale, Meenan, et al., 1994; Himmelbach & Karnath, 2005; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner et al., 2001; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Revol et al., 2003; Rice et al., 2008; Schindler et al., 2004). Importantly, aspects of this double dissociation have been demonstrated on a variety of tasks including saccades, reaching, grasping, and obstacle avoidance. It is therefore parsimonious to interpret these studies in the context of the two visual streams model, which posits that immediate motor control is mediated by the dorsal stream, yet when a delay is required this representation decays and is supplemented by a ventral stream representation.

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While the research from the patient domain shows convincingly that the ventral and dorsal streams separately subserve delayed and immediate actions, respectively, it remains unclear which regions within the ventral and dorsal streams causally contribute to this behavior. In addition, while a dissociation between immediate and delayed actions has been shown in healthy subjects at the behavioral level (Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000), it is not clear how this double dissociation is explained in the healthy brain. While the lesion data is informative in this respect, the number of patients showing the effects is small and post-lesion neuronal reorganization makes it challenging to be certain about the roles of specific brain areas in normal visuomotor performance.

Studies using neuroimaging (Binkofski et al., 1998; Culham et al., 2003; Frey, Vinton, Norlund, & Grafton, 2005), and more recently TMS (Glover, Miall, & Rushworth, 2005; Rice, Tunik, & Grafton, 2006; Rice, Tunik, Cross, & Grafton, 2007; Tunik, Frey, & Grafton, 2005) have been informative in identifying posterior parietal regions in the healthy human brain involved in grasping actions. In particular, the anterior intraparietal sulcus (aIPS) is consistently identified for its role in mediating grasping in both monkeys (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Murata, & Mine, 1995) and humans (Binkofski et al., 1998; Culham et al., 2003; Frey et al., 2005). Human aIPS is located at the junction between the postcentral sulcus and in the intraparietal sulcus (IPS) (for review see Tunik, Rice, & Grafton, 2007). In a series of recent studies, we have shown that transient TMS-induced disruption of aIPS (but not other parietal regions) impairs the online control of grasping with the contralateral hand (Tunik et al., 2005; Rice, Tunik, et al., 2006; Rice et al., 2007). In particular, we have shown that aIPS is causally involved in grasping when movement initiation *immediately* follows a ‘go’ cue or when an *immediate* movement correction to a perturbation is required (Rice, Tunik, et al., 2006). We posited (Rice, Tunik, et al., 2006) that the role of aIPS in the online control of grasping may be related to the computation of a difference vector, which is computed by determining the difference between the target vector and current position vector (Ulloa & Bullock, 2003).

Although behavioral and neuropsychological evidence suggests that delayed, but not immediate, actions recruit the ventral stream, it remains uncertain which ventral stream regions are critical. One likely candidate is the lateral occipital complex, LOC (Malach et al., 1995), which includes the lateral occipital area, LO, on the lateral surface of the occipito–temporal junction, along with other areas on the ventral occipitotemporal (VOT) surface (such as the posterior fusiform sulcus). The LOC is activated in human neuroimaging studies across a range of object perception and recognition tasks (for review see Grill-Spector, Kourtzi, & Kanwisher, 2001). Moreover, TMS to LO (Brodmann’s area 37) slows subjects’ reaction times for object picture naming (Stewart, Meyer, Frith, & Rothwell, 2001) and shape discrimination (Ellison & Cowey, 2006). Interestingly, LO is damaged bilaterally in D.F. (James, Culham, Humphrey, Milner, & Goodale, 2003), a patient with visual form agnosia who can perform visually guided grasping in real time, but not following a delay (Goodale, Jakobson, et al., 1994). D.F.’s case suggests that although immediate grasps can be performed by the dorsal stream (including aIPS, which remains intact) in the absence of LO input, delayed grasps appear to require that LO be intact. Note that D.F.’s lesions do not include all of LOC; the lateral subdivision (LO) is damaged, but the VOT subdivision is spared (James et al., 2003; Steeves, Humphrey, Culham, Menon, & Goodale, 2002; Steeves et al., 2004). Another possibility, is that some of D.F.’s deficits arise from an additional lesion in left medial parieto-occiptial cortex rather than LO (James et al., 2003). Patient M.C., who also shows impairments for delayed but not immediate grasping (Goodale et al., 2008) also has damage to LO; however, like D.F. she also has additional lesions (in this case, bilateral occipital and right parietal cortex) (Culham, Witt, Valyear, Dutton, & Goodale, 2008), making it difficult to definitively show that LO is the critical area accounting for dissociation between immediate and delayed grasping.

Evidence from functional MRI supports the suggestion that LO is involved in delayed but not immediate grasping. First, fMRI during immediate actions has indicated that aIPS is reliably activated for visually guided grasping (in which vision is used to preshape the hand) compared to reaching (in which no preshaping is required); whereas, LO is equally activated by grasping and reaching, suggesting that real-time grasping requires processing in aIPS but not LO (Cavina-Pratesi, Goodale, & Culham, 2007; Culham et al., 2003). Second, fMRI during delayed grasping has revealed reactivation of LO and early visual areas at the time of action execution, many seconds after the object was visually presented (Singhal, Kaufman, Valyear, & Culham, 2006), suggesting that LO is involved in online control of an action under delayed conditions. Activation in LO and early visual areas was no higher during the delay period than during the intertrial interval. These results suggest that while aIPS may suffice to control grasping in real-time, after a delay, information about object shape, size and orientation may be recruited from LO and early visual areas to control the grasp. If this hypothesis is true, then immediate grasping should be unaffected by TMS to LO while delayed grasping should be disrupted if the stimulation occurs once the delayed action is cued.

However, at least three other outcomes are possible. One possibility is that the reactivation of LO after a delay is merely “epiphenomenal”, perhaps occurring because subjects are imagining the objects to be grasped even if visual imagery is not essential to the success of delayed grasping. Another possibility is that delayed grasping is mediated by aIPS rather than LO. Macaque neurophysiology within area AIP (the proposed functional equivalent of human aIPS) has reported sustained activation during the delay period (Murata, Gallese, Kaseda, & Sakata, 1996), a result corroborated by human fMRI (Singhal et al., 2006). This would lead to the alternative hypothesis that TMS to aIPS would disrupt both delayed and immediate grasping but TMS to LO would disrupt neither. A third possibility is that other areas within the ventral stream besides LO are recruited by delayed grasping. Delayed grasping, in which the target and action are offset in time, may be similar in spirit to pantomimed grasping, in which the target and action are offset in space (i.e. subjects pretend to perform a grasp in a location adjacent to the object while the object remains present (Goodale, Jakobson, et al., 1994). An fMRI study of pantomimed vs. real actions found activation in another region of the ventral stream – the middle temporal gyrus – rather than LO (Króliczak, Cavina-Pratesi, Goodman, & Culham, 2007) In sum, although there is evidence to suggest that delayed grasping requires revival of object-specific information from LO, a new experiment with TMS offers the possibility to test the various hypotheses, but to make stronger arguments (than fMRI) based on the *necessity* of aIPS and LO to immediate and delayed actions.

Given the two streams theory, we tested the hypothesis that processing within aIPS and LO may be particularly important in the online control of immediate versus delayed grasping, respectively. We applied TMS to induce a “virtual lesion” to aIPS or LO at the time when subjects executed grasping movements to targets of varying size. We chose to induce stimulation at the time of action based on our prior neuroimaging results suggesting that LO is reactivated at the time of action, but not differentially activated during the delay period (Singhal et al., 2006), and because our prior TMS data has shown that aIPS becomes necessary for grasping at the time of movement execution (Rice, Tunik, et al., 2006), reflecting a specific role in the online control of the movement. The auditory cue to initiate the grasping movement either immediately followed vision of the target or occurred after a two second delay. Grasping was performed in open loop, using liquid crystal shutter glasses to control viewing time of the target. We choose this behavioral paradigm, for several reasons. First, our previous TMS investigations have confirmed that the dorsal stream is necessary for immediate grasping under these behavioral conditions (Rice, Tunik, et al., 2006; Rice et al., 2007). Second, a recent study has shown that an optic ataxia patient (with unilateral dorsal stream damage) is unable to avoid obstacles in his workspace when the movement is performed in open loop, simultaneous with visual occlusion; yet this behavior improves following a delayed response (Rice et al., 2008). Finally, we believe that this paradigm has advantages over some previous paradigms investigating delayed actions, which have involved contrasting: (1) immediate closed loop motor conditions to delayed open loop motor conditions (Milner, Paulignan, et al., 1999); (2) immediate real grasping to delayed pantomimed grasping (Goodale, Jakobson, et al., 1994; Milner et al., 2003). In our study, both the viewing time of the target and the vision of the hand and arm were identical in our immediate and delayed conditions, meaning that any differences observed could be not be accounted for by confounding influences, but instead would be related to how the movement representation (current in the case of immediate grasping; and a perceptual memory representation in the case of delayed grasping) influences the online control of the movement.

We predicted, based on the two streams model and the fMRI reactivation of LO upon action execution, that relative to the no-TMS condition, TMS-to-aIPS would interfere with grasping under immediate conditions only, whereas TMS-to-LO would interfere with grasping under delayed conditions only. Given that past studies have shown that TMS to aIPS affects the kinematic parameters of the grasp but not the transport (Rice, Tunik, et al., 2006; Rice et al., 2007; Tunik et al., 2005) we were particularly interested in the grasp-related dependent variables (maximum grip aperture and the time at which it occurred; peak velocity and the time at which it occurred). By looking at both these variables we were able to assess the TMS effects on early movement kinematics (peak velocity) and late movement kinematics (maximum grip aperture). This is particularly important as the effects of TMS are known to be transient and as such would not result in the gross behavioral deficits observed in patient studies.

2. Experimental procedure

2.1. Subjects

Nine healthy subjects participated in the study after providing written informed consent (five females, four males; mean age ± standard deviation (S.D.), 25 ± 3.6 years old). Data from one additional subject were discarded due to technical difficulties. Dartmouth Institutional Review Board approval was granted for all procedures. All subjects were right handed, as determined using the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained from each subject prior to participation in the study in accordance with the principles of the Declaration of Helsinki.

2.2. Procedure

Subjects were seated at a table and instructed to place their thumb and index finger on a start button directly in front of them. They viewed an object, positioned at shoulder level 57 cm away, mounted on the shaft of a motor (Kollmorgen model no. S6MH4). This object comprised four rectangular targets offset at 45°. Each target was 1.5 cm wide and 1 cm deep, however the length of each target varied (8, 7, 6 or 5 cm). On a trial-by-trial basis the motor rotated the object so that one of the four targets was oriented vertically. Subjects were instructed to grasp the vertically oriented object. Varying object sizes were used to force subjects to generate a new motor plan on a trial-by-trial basis. Visual feedback was controlled by liquid crystal shutter glasses (Plato System, Translucent Technologies, Canada), which were programmed to open for 200 ms at the start of each trial, and remained opaque between each trial, ensuring that the actions were in open loop. Subjects were instructed to grasp the target (which was oriented on the vertical dimension) when they heard the tone. The tone sounded, on a block-by-block basis, either simultaneous with the closing of the shutter glasses (immediate) or two seconds after the glasses closed (delayed). The object was to be grasped using a precision grip, with the index finger and thumb. The object was not to be removed from the motor, subjects simply had to grasp the object briefly then release their grip and return to the start position. Although some past studies have investigated target perturbations (Rice, Tunik, et al., 2006; Tunik et al., 2005), no such perturbations occurred in this experiment. Subjects grasped the target while they received TMS to their left aIPS, left LO or not at all. As such, there were six different conditions, presented in blocks in a counterbalanced order: (1) no-TMS, Immediate grasp; (2) no-TMS, Delayed grasp; (3) TMS-to-aIPS, Immediate grasp; (4) TMS-to-aIPS, Delayed grasp; (5) TMS-to-LO, Immediate grasp; (6) TMS-to-LO, Delayed grasp. Each block consisted of 40 trials, with an equal probability of each of the four target objects being oriented on the vertical dimension on any given trial, forcing subjects to make a movement plan during the viewing period of each trial. In TMS trials, the TMS was delivered in double pulses, with the first pulse (TMS 1) delivered simultaneous with the release of the start button, and the second pulse (TMS 2) occurring 100 ms after the first (see Fig. 1). This double-pulse sequence was used to lengthen the window during which the TMS-induced virtual lesion affected function. This sequence has proven effective in similar TMS paradigms (Rice, Tunik, et al., 2006; Rice et al., 2007). It should be noted that TMS was delivered simultaneous with start of the movement in both immediate and delayed conditions and as such all effects will be restricted to online control of the movement, and not in movement planning. The only difference between the immediate and delayed conditions was the representation the movement was based upon – current or real-time information in the case of immediate grasping, and a perceptual memory representation in the case of delayed grasping. We were specifically interested in the role of these representations on the online control of a grasp.

2.3. Localization of brain sites and TMS

Two cortical sites were chosen for stimulation: (1) the most anterior region of the IPS in the left hemisphere (aIPS) (Culham et al., 2003; Frey et al., 2005); (2) the lateral occipital (LO) area in the left hemisphere, as detailed in Fig. 2. TMS is well-known for its good temporal and spatial resolution, although some evidence suggests that it may influence areas outside the stimulation locus (Bestmann et al., 2008). It is worth noting, however, that our previous investigations have shown that the influence of aIPS on grasping is focally specific, with TMS induced deficits not being observed in right-handed grasping when applied to other regions along the intraparietal sulcus (Rice, Tunik, et al., 2006), or to the same region in the ipsi-lateral hemisphere (Rice et al., 2007). Earplugs were provided to dampen the noise associated with the discharge from the TMS coil as well as the rotation of the motor.

A full-brain T1-weighted image was acquired using a spoiled gradient recalled three-dimensional sequence (repetition time, TR = 9.9 ms; time to echo, TE = 4.6 ms; flip angle = 8°; field of view, FOV = 240 mm; slice thickness = 1 mm; matrix = 256 × 256) on each subject (Philips 3T MRI scanner), and the cortical surface was displayed as a three-dimensional representation using Brainsight Frameless Stereotaxic software (Rogue-Research, Montreal, Quebec, Canada). Each targeted cortical site was demarcated on the

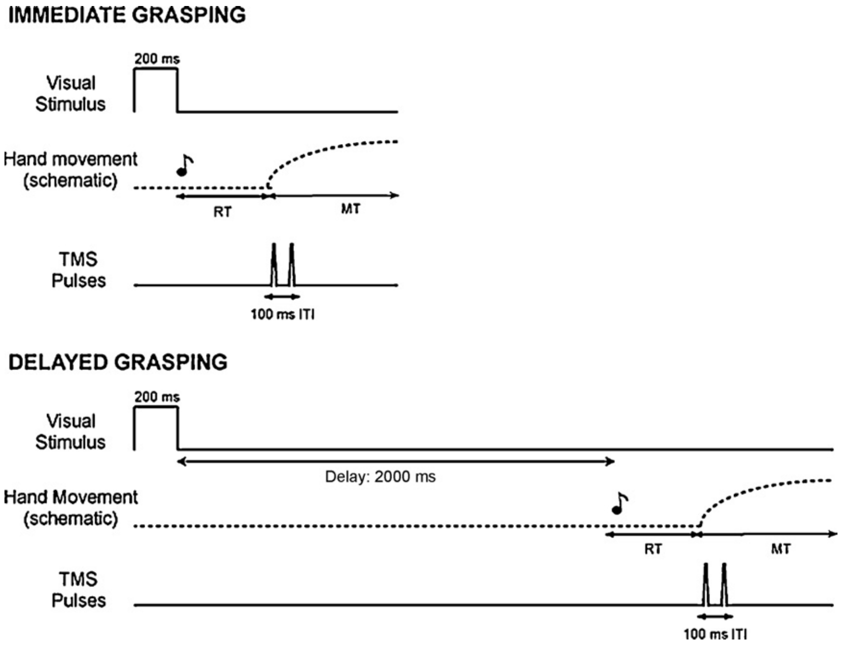

Fig. 1. Experimental set-up. Schematic of experimental timing for the immediate grasping and delayed grasping conditions. Shutter glasses opened for 200 ms at the start of each trial, enabling subjects to briefly view the object mounted on the motor before closing so that the action was performed in open loop (i.e. without vision). Under immediate conditions the 'Go' cue (indicated by the music note icon) sounded simultaneous with closing of the shutter glasses. Under delayed conditions the 'Go' cue sounded two seconds after the glasses closed. On hand movement onset (signalled by release of the start button) the first TMS pulse was delivered, followed by the second pulse 100 ms later. Approximate reaction time (RT) and movement time (MT) are indicated.

three-dimensional image using the same software. The position of the coil and the subject's head were monitored using a Polaris Optical Tracking System (Northern Digital, Inc., Waterloo, Ontario, Canada). Positional data for both rigid bodies were registered in real-time to a common frame of reference and were superimposed onto the reconstructed three-dimensional MRI image of the subject using the Brainsight software. For both sites, the TMS coil was held tangential to the surface of the skull, with the handle pointing backwards. The coil was held to the subject's skull by the experimenter using one hand, with the other hand stabilizing the head to the coil. The position of the coil to the head was monitored continuously online using Brainsight, and head movements were judged to be negligible.

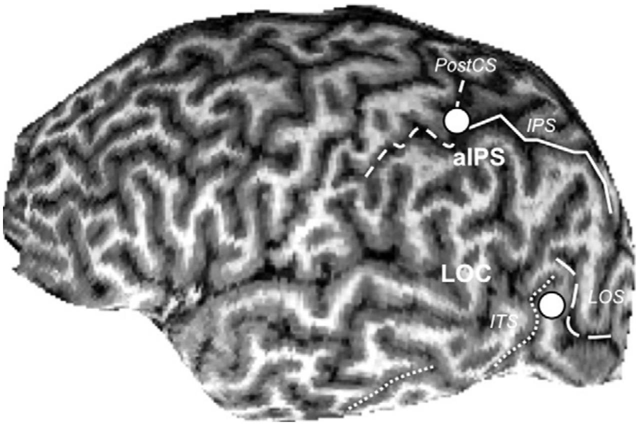

Fig. 2. Localization of brain sites for TMS. A three dimensional rendering of one subject's structural MRI in Brainsight, illustrating the cortical sites chosen for stimulation, as indicated by the white dots: (1) the anterior intraparietal sulcus, aIPS, site was located at the junction of the anterior intraparietal sulcus, (IPS, solid line), and the postcentral sulcus (PostCS, dashed line); (2) the lateral occipital, LO, site was near the junction of the inferior temporal sulcus (ITS, fine-dashed line) and lateral occipital sulcus (LOS, coarse-dashed line). Area MT+ lies at the junction of the two sulci (Dumoulin et al., 2000) and intersubject comparisons of MT+ and LO foci from an fMRI study (data provided by Tutis Vilis; see also Large, Aldcroft, & Vilis, 2005, 2007) suggest that LO typically lies approximately posterior and inferior to MT+ (average Talairach coordinates: MT+ −44, −62, −2; LO −45, −69, −6). Thus in most subjects, we placed the LO site slightly inferior and posterior to the sulcal junction (although in the subject shown, the trajectory of the LOS limited anterior–posterior placement of LO).

A Neotonus PNS Stimulator (model no. N-0233-A-110 V) (Neotonus Inc., GA) with an air cooled iron-core butterfly-shaped coil was used to administer TMS. Pulse duration for this stimulator and head coil is 180 μs (at 100% of operating power). Double-pulse TMS (inter-stimulus interval, 100 ms) was applied at 110% of motor threshold, to both sites. Motor threshold was defined as the intensity required to produce a visible contraction of the intrinsic hand muscles of the right hand 50% of the time with the coil positioned over the hand area of the left primary motor cortex.

After completing the experiment all participants were required to complete a side effects questionnaire, as recommended by Machii, Cohen, Ramos-Estebanez, and Pascual-Leone (2006). No side effects attributable to TMS were reported by any of the subjects. One subject reported shoulder ache by the end of the experiment, which was attributed to the task rather than the TMS.

2.4. Analysis and statistics

Kinematic data were obtained by localizing the three-dimensional position of three infrared light-emitting diodes (Optotrak 3020, Northern Digital Inc., Canada; sampling rate, 100 Hz) attached to the tip of the index finger, thumb, and the metacarpophalangeal joint (MPJ) of the index finger of the right hand. Offline, missing samples were interpolated and the data were filtered at 10 Hz using custom written LabVIEW (National Instruments, Austin, Texas) software. The onset and offset of the movement were defined as the time at which the velocity of the MPJ marker exceeded and then fell below 50 mm/s, respectively. Trials were excluded from the analysis if data points were missing due to occlusion of the infrared light-emitting diodes. Trials were also excluded from analysis if reaction times exceeded 800 ms in the immediate grasping condition or were initiated prior to the auditory “Go” cue (2000 ms after the visual cue) in the delayed grasping condition. A total of 7.55% of trials were excluded from the analysis. For the valid trials, average reaction time for immediate conditions (averaged across TMS condition) was 387.13 ms after the “Go” cue; for delayed conditions, average reaction time was 649.65 ms after the “Go” cue. Note that TMS was not delivered until the movement was initiated and therefore would have no effect on reaction time measures, thus this variable was not included as a dependent measure.

Kinematic data were analyzed separately for the transport and grasp components of the movement. Separate analysis of transport and grasp components of a prehensile movement has been carried out in other TMS grasping studies, and has suggested that transport and grasp are subserved by different neural substrates (Rice, Tunik, et al., 2006; Rice et al., 2007; Tunik et al., 2005). Transport-related dependent measures were indicated by a “t” suffix and included: Movement Time (MTt) defined as the duration between movement onset and offset; Peak Velocity (PVt) defined as the maximum value of the first derivative of the 3D position of the MPJ marker; Time to Peak Velocity (%TPVt) defined as the time interval between peak velocity and movement onset, expressed as a percentage of movement time. Grasp-related dependent measures were indicated by a “g” suffix and included: Maximum Grip Aperture (MGAg) defined as the three-dimensional distance between the index and thumb markers; Time to Maximum Grip Aperture (%TMGAg) defined as the time interval between MGA and movement onset, expressed as a percentage of movement time; Peak Velocity of Grip Aperture (PVg) defined as the maximum value of the first derivative of grip aperture; Time to Peak Velocity of Grip Aperture (%TPVg) defined as the time interval between peak velocity of grip aperture and movement onset, expressed as a percentage of movement time.

Data were analyzed using 3 × 2 × 4 repeated measures analysis of variance (ANOVA) for each dependent measure, with factors TMS site (TMS-to-aIPS, TMS-to-LO and no-TMS), time (Immediate and Delayed) and object size (8, 7, 6 and 5 cm). Huynh–Feldt corrections were applied where sphericity assumptions were violated. Wherever significant results were obtained, *t*-tests were used for subsequent analysis. A significance threshold of 0.05 was adopted. For conciseness only significant findings are discussed, however data for all variables are presented in Table 1.

3. Results

3.1. Grasp component

A significant interaction was observed between TMS and time for the peak velocity of the opening of the hand, PVg ($F_{(1.167,\,9.332)} = 7.795$, $p = 0.018$). Paired sample *t*-tests (comparing TMS to the corresponding no-TMS conditions) were conducted to determine the source of this interaction (Fig. 3a). Results revealed that, compared to the no-TMS condition (231.9 mm/s), TMS-to-LO (253.27 mm/s) resulted in higher PVg under delayed movement conditions ($t = -5.333$, d.f. = 8, $p = 0.001$). There was no significant difference between the no-TMS condition (229.15 mm/s) and TMS-to-LO (234.37 mm/s) for immediate movement conditions ($t = -0.607$, d.f. = 8, $p = 0.561$). TMS-to-aIPS (244.41 mm/s) had no

Table 1
Results.

	MTt	PVt	%TPVt	MGAg	%TMGAg	PVg	%TPVg
No TMS							
Immediate							
5 cm	815.21 (146.53)	1175.10 (207.14)	35.23 (4.31)	67.61 (7.51)	73.20 (5.96)	203.61 (30.56)	35.99 (6.58)
6 cm	794.51 (141.09)	1203.74 (203.15)	35.44 (4.51)	71.88 (7.52)	76.52 (5.66)	216.75 (32.82)	37.21 (7.36)
7 cm	812.29 (139.39)	1206.25 (218.52)	34.95 (4.81)	75.53 (6.53)	72.80 (9.91)	234.36 (43.86)	36.02 (7.30)
8 cm	800.79 (138.43)	1193.03 (214.52)	35.68 (4.79)	80.64 (8.48)	72.74 (10.32)	261.86 (54.48)	35.45 (6.60)
Delayed							
5 cm	796.22 (143.06)	1203.51 (232.84)	34.84 (3.92)	70.94 (8.26)	74.47 (7.08)	216.33 (34.09)	36.43 (5.43)
6 cm	821.54 (168.06)	1185.16 (221.97)	35.38 (5.01)	73.05 (7.91)	73.39 (9.28)	222.73 (35.26)	37.84 (6.13)
7 cm	833.65 (153.84)	1184.40 (213.13)	34.80 (5.84)	75.95 (7.40)	71.40 (8.46)	237.70 (43.40)	35.65 (8.43)
8 cm	843.38 (165.71)	1189.69 (235.11)	34.75 (4.75)	80.53 (8.03)	73.53 (9.49)	250.84 (50.86)	36.26 (6.81)
aIPS TMS							
Immediate							
5 cm	797.85 (117.86)	1233.08 (191.72)	35.74 (5.37)	72.27 (11.82)	69.79 (11.86)	239.31 (63.65)	31.73 (8.50)
6 cm	793.29 (138.19)	1230.11 (188.56)	34.65 (4.68)	73.70 (11.82)	70.44 (12.50)	244.09 (68.00)	31.33 (8.82)
7 cm	786.85 (113.79)	1247.05 (171.92)	34.33 (4.68)	77.23 (11.38)	70.91 (14.31)	263.70 (70.76)	30.94 (8.56)
8 cm	772.20 (146.44)	1244.30 (185.50)	35.58 (5.51)	82.01 (11.84)	72.77 (14.58)	278.80 (78.52)	29.79 (8.93)
Delayed							
5 cm	813.17 (108.91)	1219.35 (188.71)	35.75 (5.82)	73.38 (10.29)	71.96 (13.07)	227.99 (53.42)	32.42 (9.25)
6 cm	823.60 (125.20)	1216.21 (203.61)	35.95 (6.68)	74.02 (9.60)	70.06 (14.30)	236.54 (60.23)	31.82 (11.13)
7 cm	804.28 (133.68)	1201.09 (206.72)	36.43 (5.41)	78.12 (10.27)	71.68 (12.61)	250.64 (68.63)	32.89 (9.04)
8 cm	792.23 (116.66)	1225.43 (208.60)	37.45 (5.60)	81.50 (10.25)	73.40 (12.76)	262.46 (72.58)	33.23 (9.83)
Lo TMS							
Immediate							
5 cm	765.15 (115.30)	1230.39 (199.07)	35.64 (3.81)	69.57 (8.57)	71.94 (8.33)	215.68 (43.55)	36.41 (8.91)
6 cm	757.26 (113.40)	1263.51 (182.50)	35.57 (3.42)	71.27 (9.36)	74.26 (4.12)	220.54 (49.66)	33.73 (6.36)
7 cm	774.49 (125.66)	1252.54 (194.82)	35.72 (5.17)	76.79 (6.80)	73.14 (10.02)	241.44 (45.98)	34.00 (7.62)
8 cm	748.22 (107.21)	1260.56 (197.51)	36.30 (4.75)	79.97 (8.59)	74.43 (9.14)	259.80 (52.63)	34.78 (6.69)
Delayed							
5 cm	767.05 (93.23)	1266.92 (194.04)	35.02 (3.83)	75.03 (6.86)	69.77 (6.16)	241.47 (29.97)	35.02 (6.63)
6 cm	746.69 (143.86)	1273.31 (203.29)	36.13 (4.63)	76.05 (7.36)	71.76 (4.93)	244.40 (32.01)	35.27 (5.51)
7 cm	789.43 (143.66)	1249.88 (205.22)	35.78 (4.51)	79.22 (6.87)	71.39 (8.25)	254.56 (41.57)	34.33 (8.71)
8 cm	734.29 (127.34)	1268.32 (208.12)	37.95 (3.66)	82.48 (7.12)	74.58 (7.85)	272.65 (39.60)	36.49 (7.16)

The table depicts mean and standard deviations (shown in parentheses) for all the dependent variables, including movement time (MTt), peak velocity of wrist (PVt), time of peak velocity of wrist (%TPVt), maximum grip aperture (MGAg), time of maximum grip aperture (%TMGAg), peak velocity of grasp (PVg) and time of peak velocity of grasp (%TPVg).

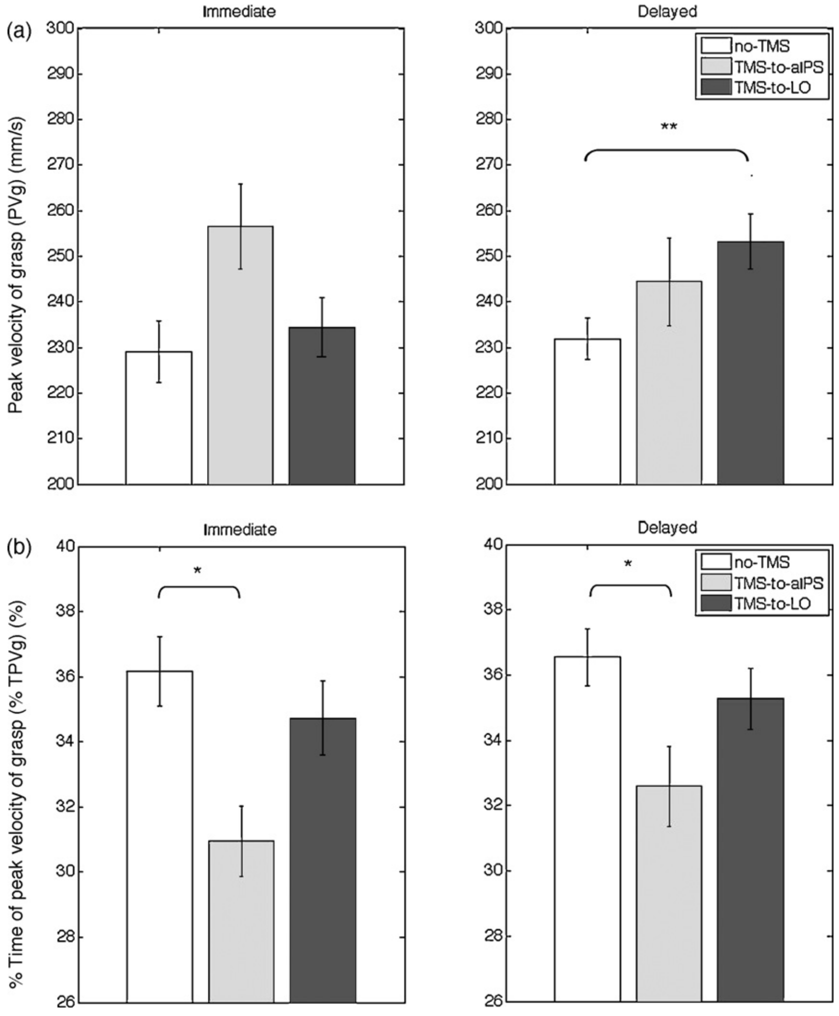

Fig. 3. Results. Graphs depict significant findings for the grasping component of the movement, including: (a) peak velocity (PVg); (b) time of peak velocity (%TPVg). The left panel shows data from the immediate grasping conditions, and the right panel shows data from the delayed grasping conditions. Bars indicate means, error bars represent within subject standard error, $^{*}p < 0.05$, $^{**}p < 0.01$.

significant effects on PVg for delayed grasping ($t = -0.944$, d.f. = 8, $p = 0.373$), although there was a non-significant trend ($t = -1.869$, d.f. = 8, $p = 0.098$) towards an increase in PVg for immediate grasping for TMS-to-aIPS (256.48 mm/s).

A significant main effect of TMS was observed for the time at which the peak velocity of the hand aperture was reached, %TPVg ($F_{(1.547, 14.775)} = 5.783$, $p = 0.015$). Paired samples t-tests comparing TMS-to-aIPS and TMS-to-LO to the no TMS condition, revealed that this difference can be accounted for by a significantly earlier %TPVg for TMS-to-aIPS (31.77%) when compared to no-TMS (36.36%), ($t = 2.803$, d.f. = 8, $p = 0.023$), but not TMS-to-LO (35%), ($t = 1.407$, d.f. = 8, $p = 0.197$) (Fig. 3b).

A significant main effect of object size was found for the variables PVg ($F_{(1.195, 9.559)} = 12.957$, $p = 0.004$) and MGAg ($F_{(1.354, 10.831)} = 17.743$, $p = 0.001$). This can be accounted for by an increase in each of these variables as object size increases (see Table 1). A significant interaction between time and object size was observed for the variables PVg ($F_{(3, 24)} = 4.293$, $p = 0.015$) and MGAg ($F_{(2.114, 16.915)} = 4.647$, $p = 0.023$). To determine the source of this interaction, paired sample t-tests were conducted comparing immediate and delayed grasping conditions for each object size. For all the above variables, the only significant difference between immediate and delayed conditions was for the 5 cm object, where MGAg was smaller for immediate (69.82 mm) than delayed (73.12 mm) conditions ($t = -3.859$, d.f. = 8, $p = 0.005$).

A significant interaction between TMS and object size was observed for %TMGAg ($F_{(6, 48)} = 2.839$, $p = 0.019$). Paired sample t-tests, comparing each condition to the corresponding no-TMS condition revealed no significant differences ($p > 0.114$ for all comparisons).

3.2. *Transport component*

The transport component of the movement was analyzed for control purposes. For the transport dependent variables, a significant effect of TMS was observed for the total movement time, MTt ($F_{(2, 16)} = 4.816$, $p = 0.023$). Paired sample t-tests reveal that the TMS main effect can be accounted for by a significantly shorter MTt for the TMS-to-LO condition (760.32 ms), compared to no-TMS (814.70 ms), ($t = 2.879$, d.f. = 8, $p = 0.021$), but not TMS-to-aIPS (797.93 ms), ($t = 0.808$, d.f. = 8, $p = 0.442$).

A significant interaction was observed for TMS by size for MTt ($F_{(6, 48)} = 3.654$, $p = 0.005$); this can be accounted for by a significant difference between no-TMS and TMS-to-LO for object size 6 cm ($t = 3.691$, d.f. = 8, $p = 0.006$) and 8 cm ($t = 3.802$, d.f. = 8, $p = 0.005$) only, although it should be noted that there was a trend towards significance for the 7 cm object ($p = 0.066$) and the 5 cm ($p = 0.163$). A significant interaction between time and object size was observed for PVt ($F_{(2.982, 23.854)} = 5.587$, $p = 0.005$). To determine the source of this interaction, paired sample t-tests were conducted comparing immediate and delayed grasping conditions for each object size. This revealed no significant differences ($p > 0.114$ for all comparisons).

4. Discussion

Here we have found a dissociation whereby TMS to aIPS and LO led to different effects on kinematic measures associated with hand preshaping under delayed and immediate grasping conditions. Specifically, TMS to LO under delayed movement conditions led to an increase in the peak velocity of the hand opening (PVg) and TMS to aIPS results in earlier time of peak velocity of hand opening (%TPVg) under immediate and delayed conditions. Although velocity has not been widely studied in the kinematic literature, we previously reported TMS-induced disruption of both peak velocity (Rice, Tunik, et al., 2006) and its timing (Rice et al., 2007) when TMS was applied to aIPS during immediate grasping (see Table 2), a result supported by a findings in the present experiment.

Peak velocity measures are important (though perhaps underemphasized) components of grasp kinematics. PVg is known to increase with object size and MGAg (Paulignan, Jeannerod, Mackenzie, & Marteniuk, 1991; Saling, Mescheriakov, Molokanova, Stelmach, & Berger, 1996; Tretriluxana, Gordon, & Winstein, 2008), presumably because larger objects require larger grips, so the hand must open more quickly to reach MGAg in a similar time period (TMGAg). Indeed, we observed an increase in PVg with TMS-to-LO during delayed grasping (and a trend towards an increase in PVg with TMS-to-aIPS during immediate grasping). Also, when there is greater uncertainty in the grasp, the hand may open more quickly (i.e. TPVg may increase) to enable a slower closure of the hand as it approaches the object. Indeed, this effect occurred for stimulation of aIPS for both immediate and delayed grasping. This replicates our past work showing the effect for immediate grasping (Rice et al., 2007), and extends it to delayed grasping. This finding is of particular interest when compared to the optic ataxia literature, which shows that patients suffering from optic ataxia exhibit a longer deceleration phase (i.e. longer hand closure) to accomplish a movement (Grea et al., 2002; Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1986).

Although it initially appears surprising that TMS affects PVg and TPVg, but not MGAg, this may be explained by the fact that the effects of TMS are transient in nature and are strongest immediately following administration of the pulses. If this were true, we would expect the effects of TMS to be strongest on dependent variables occurring closest to TMS stimulation. Table 2 provides a summary of the findings from the current study and our two previous published studies investigating the role of aIPS in the online control of grasping movements (Rice, Tunik, et al., 2006; Rice et al., 2007). This table shows that our current and previous results support a time-dependence of TMS-induced interference on the kinematics of grasping, with TMS-to-aIPS disrupting only kinematic variables that are measured within approximately 350 ms of administration of the pulses. This would explain why the changes in the present study are evident only for peak velocity measures. It should be noted that there are differences in the experimental paradigms employed across studies; for example, in Rice, Tunik, et al. (2006) subjects reached to grasp a target that could change size or not, unpredictably, after movement onset, whereas, in Rice et al. (2007) subjects reached to grasp a differently-sized target on each trial. Such methodological differences may contribute to differences in the precise patterns of findings between studies.

Our results clarify some of the confusion that has arisen from past results using other techniques. Studies have suggested that neurologically intact subjects require ventral stream processing for delayed but not immediate grasping, a conclusion proposed on the basis of neuropsychological patients (Goodale, Jakobson, et al., 1994; Goodale, Meenan, et al., 1994; Himmelbach & Karnath, 2005; Milner, Dijkerman, et al., 1999; Milner, Paulignan, et al., 1999; Milner et al., 2001, 2003; Revol et al., 2003; Rice et al., 2008; Schindler et al., 2004). Our results propose that a specific area within the ventral stream – the lateral occipital area – plays a role in recalling visual information to control an action online following a delay, consistent with a proposal based on fMRI in neurologically intact subjects (Singhal et al., 2006). In addition, our present results demonstrate the importance of the fMRI reactivation that arises in LO when a delayed action is cued. That is, the fact that grasping was influenced by LO stimulation argues strongly that the LO reactivation is not merely an epiphenomenon due to non-essential factors such as mental imagery of the action (as do recent follow-up fMRI experiments that included a grasping imagery condition (Monaco, McAdam, McLean, Culham, & Singhal, 2008)).

It is important to note that our study only investigated the role of aIPS and LO in the *online control* of the movement. Our evidence that LO is involved in the online control of the movement under delayed movement conditions may seem at odds with the traditional definition of the role of the ventral stream in delayed actions,

Table 2
Summary of current and previous findings.

Study	TMS site	Condition	Variable	Peak time – TMS time	p
Rice, Tunik, et al. (2006)	Left aIPS	No perturbation	PVg	–[a]	0.084
			TMGAg	**362.23**	0.048
	Left aIPS	Perturbation	PVg	–[a]	0.017
			MGAg	**187.71**	0.005
Rice et al. (2007)	Left aIPS	Right hand	%TPVg	**140.75**	0.004
			MGAg	483.84	ns
	Right aIPS	Left hand	%TPVg	**138.06**	0.042
			MGAg	542.4	ns
Current findings	Left aIPS	Immediate	%TPVg	**191.42**	0.023
			MGAg	494.77	ns
		Delay	%TPVg	**201.23**	0.023
			MGAg	502.95	ns
	Left LO	Immediate	PVg	191.42	ns
			MGAg	494.77	ns
		Delay	PVg	**201.23**	0.001
			MGAg	502.95	ns

The table depicts a summary of our previously observed findings, including significance levels revealed by post-hoc comparisons. We report the difference in time between the final pulse of TMS and the time of the observed effects; this difference is based on the no TMS condition in the corresponding study. Significant findings always occur within approximately 350 ms (highlighted in bold) of the final TMS pulse.

[a] In Rice, Tunik, et al. (2006) we did not report the timing of PVg, however it should be noted that in all our studies PVg always occurs approximately 300 ms before MGAg.

which might seem to imply that the ventral stream is only involved in “offline” control of action. The difference between immediate and delayed movement conditions is with regards to the representation that the action is based upon – a real-time representation in the case of immediate action, and a perceptual memory representation in the case of delayed actions. For *both* immediate and delayed grasps the actions must be controlled online to ensure successful completion of the movement. This online control is thought to involve the computation of a difference vector (Ulloa & Bullock, 2003), which involves a comparison between the target aperture (which is based on the action representation) and the current aperture (which is based on continuous feedback). Our data suggests that aIPS is involved in this computation under immediate conditions, suggesting that the target aperture and current aperture are processed within dorsal stream regions. However, under delayed movement conditions additional processing is required from the ventral stream, presumably because the dorsal stream representation of the target aperture (i.e. object size) has decayed and is instead represented by a perceptual memory representation from the ventral stream. Our finding thus represents an extension of the Milner and Goodale model, by suggesting that ventral stream area LO and dorsal stream area aIPS interact to control a movement online under delayed movement conditions.

Our results support findings with visual form agnosia patients showing that a delay before response results in impaired grasping (Goodale, Jakobson, et al., 1994), suggesting that the ventral stream contributes to grasp under delayed movement conditions. Our results, however, suggest that the ventral stream cannot completely compensate for a defective dorsal stream (and vice versa) when performing delayed movements, since TMS to aIPS and LO both influenced grasping in the delayed condition. Such an explanation may explain why, in spite of some improvement in motor performance under delayed conditions, optic ataxia patients’ accuracy does not normalize to healthy subjects’ levels (Milner, Paulignan, et al., 1999). In other words, even though a delayed movement can augment optic ataxia patients by recruiting ventral stream processes, motor performance remains suboptimal.

Our findings help to reconcile the paradox that, according to macaque physiology, AIP stores information over the delay (Murata et al., 1996), while according to human neuropsychology, this information on its own is insufficient to enable accurate grasping. That is, AIP may be storing some but not all of the information necessary to control a delayed action. Our results suggest that under delayed movement conditions both aIPS and LO are required to control the movement online; this may reflect a role of LO in the perceptual memory representation of the expected (target) aperture, and a role of aIPS in computing the current aperture and contrasting it to the target aperture to compute the difference vector. While information about the visual attributes of a previously seen target object appears to be recalled in LO at the time of action in order to control the movement online, a process that can be influenced by TMS, it remains to be seen whether a virtual lesion to LO during the delay period, or during initial stimulus encoding, also disrupts grasping. However, the absence of fMRI activation in LO and the presence of activation in aIPS during the delay suggests that LO stimulation would have no effect while aIPS stimulation may disrupt some components of the action. These questions require further investigation.

Our results provide some support for previous research showing kinematic differences in immediate and delayed grasping. For example, Hu et al. (1999) contrasted open loop immediate to delayed grasps and found that delayed grasps took longer and achieved peak velocity earlier. Analysis of the no TMS conditions in our study reveals a significant main effect of time, as subjects take significantly longer to perform their movements under delayed (823.70 ms) compared to immediate (805.7 ms) movement conditions ($F_{(1,8)} = 6.366$, $p = 0.036$). A significant interaction between time and size was also present ($F_{(2.520,20.163)} = 4.234$, $p = 0.022$) however, suggesting that this effect was driven by the largest object size ($t = -3.252$, d.f. = 8, $p = 0.012$). A significant interaction between time and size was also observed for PVg ($F_{(2.421,19.371)} = 3.794$, $p = 0.034$), with subjects achieving higher PVg under delayed movement conditions for the smallest object (216.33 mm/s) compared to immediate (203.61 mm/s). In sum, our results provide some support for findings showing different movement kinematics for immediate versus delayed grasping. Specific differences between the results of Hu et al. (1999) and our work can be accounted for by differences in experimental paradigm, which include differences in viewing time, object size and delay interval.

One important caveat concerns our interpretations. For the immediate grasp condition, the cue to initiate the action occurred simultaneous with the offset of the visual stimulus (Fig. 1). Based on effects upon a visual illusion, Westwood and Goodale (2003), have suggested when the action is cued at a time when the stimulus is not visible, the system may depend not on real-time mechanisms (presumably in the dorsal stream) but on perception-based memory mechanisms (presumably in the ventral stream). By this account, both our nominally “immediate” and “delayed” grasping conditions should depend on the integrity of the ventral stream. Despite this prediction, we nevertheless see that disruption of ventral stream area LO affects only delayed grasping. How can we reconcile the predictions from Westwood and Goodale with our results? First, Himmelbach and Karnath (2005) have argued, based on reaching data from optic ataxia patients, that the transition from dorsal to ventral control of actions is gradual and linear rather than abrupt. Based on this observation, we might have expected a larger difference between immediate and delayed grasping had the “Go” cue preceded vision of the target in immediate trials, however, the contribution of LO should still be *stronger* in our delayed condition. Second, recent findings of delayed obstacle avoidance behavior in an optic ataxia patient (Rice et al., 2008) have shown that an optic ataxia patient had impaired performance when required to reach between two obstacles under immediate conditions where the “Go” cue occurs simultaneously with occlusion of the shutter glasses (which is an identical immediate condition to the one employed within this study). This impairment disappears when a delay is required before response (Rice et al., 2008). Finally, consistent with the absence of an abrupt transition from dorsal to ventral visuomotor control, thus far our lab has been unable to see any fMRI activation differences dependent on whether or not the a stimulus to be grasped is visible at the time of the cue, as Westwood and Goodale would predict (Chinellato, Singhal, & Culham, unpublished pilot data, $n = 3$). In sum, there is strong evidence from our data and previous studies that our immediate grasping condition can be differentiated from our delayed condition, with delayed but not immediate grasping relying on a perceptual representation from the ventral stream.

It has been suggested that the transport and grasp components of a prehensile movement, although temporally coupled, are subserved by different neural pathways (Jeannerod, 1981, 1984). The transport component of a prehensile movement has been proposed to involve the spatial, egocentric aspects of an action, whereas the grasp component involves intrinsic aspects of object, including shape and size (Jeannerod, Paulignan, & Weiss, 1998). Our previous data have provided some support for the suggestion that the transport and grasp components of a prehensile movement are independent, with aIPS being specifically involved in the grasp component of the movement, but not transport (Rice, Tunik, et al., 2006; Rice et al., 2007). This study supports these previous findings.

While our results may surprisingly seem to show that LO contributes to the transport component of the movement (with TMS to LO disrupting MTt), we believe that caution must be used in interpreting our results this way, due to the experimental paradigm employed. In particular, while the grasp component of the movement required re-computation on a trial-by-trial basis, necessitated by varying object size, the transport component of the movement remained constant. The fact that the transport component remained constant allowed subjects to rely on a perceptual memory representation of the distance and location of the target, thus allowing them to employ a default transport movement. We propose that our results show, as would be predicted, that LO is involved where subjects are utilizing a perceptual memory representation, and it is this which accounts for the LO TMS-induced influences on the transport component of the movement. Further research needs to be carried out to determine the neural substrates of the transport component of a prehensile movement, and such studies would require an experimental paradigm manipulating the distance and/or location of the target to force subjects to control the transport component of the movement online.

In conclusion, our results have important implications for Milner and Goodale's model of the two visual streams. According to their theory, the dorsal stream mediates actions in real-time, however, under delayed movement conditions the dorsal stream representation decays and actions become mediated by the ventral stream. Our study suggests that there are ventral and dorsal stream contributions to grasping movements, with the ventral stream contributing to grasping under delayed movement conditions and the dorsal stream contributing to grasping under both immediate and delayed movement conditions. While our results provide some support for Milner and Goodale's model, we suggest that some refinement of the model is necessary to account for these new findings. In particular, we propose that under immediate movement conditions the dorsal stream controls a grasp online, by evaluating the actual grip aperture compared to the target grip aperture based on real-time information. However, under delayed movement conditions, in addition to dorsal stream involvement, the ventral stream is also required for the online control of a grasp, as the target grip aperture is based on a perceptual memory representation. The fact that aIPS contributes to grasping under immediate and delayed conditions may suggest that it is here, in the dorsal stream, that perceptual and action information merge to achieve successful motor control.

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