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Motor facilitation following action observation: A behavioural study in prehensile action

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Abstract

Previous research has shown that the observation of actions and the execution of actions activate common neural systems. More recently, we have presented data showing that action observation of prehension primes subsequent execution (Castiello et al. 2002). In the current paper we examined action priming under conditions in which the size of the prime did not predict the size of the target (only 20% of trials were valid). We demonstrated reliable priming under these conditions, consistent with the effect occurring automatically. In addition, we show priming even when observers saw just the object rather than the object and a reaching action on the prime trial. We discuss the findings in relation to the role of mirror neurons and object affordances.

Introduction

Recent research has shown evidence that the observation of actions and the execution of actions activate common neural systems. The first data to show this came from the neural measurement of area F5 in the ventral premotor cortex of monkeys (di Pellegrino et al. 1992, Gallese et al. 1996, Rizzolatti et al. 1996a). These studies demonstrated the existence of neurons that were active when a monkey observed a directed action to an object and also when the animal executed an action itself to the same object. Rizzolatti coined the term mirror neurons to describe their sensitivity to combined self and observed action (see Rizzolatti & Arbib, 1998). Observation of the object without the action, or the action without the object evoked no such response (Gallese et al. 1996). Later work by Gallese and colleagues has shown neurons with similar properties in the inferior parietal lobe of monkeys (Fogassi et al. 1998, Gallese et al. 2002).

Evidence that a mirror-neuron system may operate in humans comes from studies using transcranial magnetic stimulation (TMS) and from brain imaging studies. Fadiga et al. (1995) stimulated the motor cortex of participants with TMS to induce motor-evoked potentials (MEP's) in the muscles of the hand. They then presented participants with four observation conditions: (i) the experimenter reaching and grasping an object, (ii) the experimenter performing aimless arm movements, (iii) just an object and (iv) the observation of a dimming light. The results showed that the observation of the experimenter performing an action (reach and grasp or aimless arm movement) increased the MEP activity of the hand. They suggested that this was due to action observation

being associated with action execution processes (for replications of these findings see Hari et al. 1998, Strafella and Paus 2000, Avikainen et al. 2002). Evidence from functional imaging studies also demonstrates that the observation of actions activate the premotor cortex in humans (Broca's area) (Grafton et al. 1996, Rizzolatti et al. 1996b, Decety et al. 1997, Hari et al. 1998, Grezes et al. 1998, Iacoboni et al. 1999, 2001, Buccino et al. 2001, Chaminade et al. 2002). This premotor activation may correspond to activity observed in area F5 with monkeys.

Assuming that the mirror neuron system is present in humans, we might assume that observation of an action could influence the subsequent execution of the same action in humans, since overlapping neural circuits would be involved in the two cases. Some behavioural studies have already reported evidence of this (Brass et al. 2000, 2001ab for simple finger movements and Castiello et al. 2002 in a prehension task). Brass et al. (2000) showed that initiation of movement execution was facilitated following movement observation, relative to when responses were cued symbolically (instructed to move finger 1 or 2) or spatially (an x marked on the participants nail). Moreover, reduced similarity between the observed and executed action (i.e., when the observed action was a finger lift and the executed action was a finger tap) reduced the facilitatory effect on movement execution. Compatibility between the observed and the executed action facilitated the initiation of movement execution. More recently, we have presented data showing that action observation of prehension facilitates subsequent execution (Castiello et al. 2002). Participants observed a grasp action directed to an object and then had to grasp either the same or a different object. The object could either be small or large. We termed an observation that led to a compatible response (i.e., observe an action to the

small object and then execute an action to the small object) as a valid prime and an observation leading to an incompatible response (i.e., observe an action to the small object and then execute an action to the large object) as an invalid prime. In the first two experiments, the ratio between the valid and invalid prime trials was 80:20 and 50:50 respectively. We found that prime validity affected the dependent measures of time to peak velocity, time to peak deceleration, time to peak grasp aperture and peak grasp aperture. Components of the actions (time to peak velocity and to peak deceleration) occurred earlier for valid than invalid prime trials. Also, the time to peak grasp aperture and peak grasp aperture itself were reduced after a valid prime. The faster reach components and the smaller grasp aperture were taken as indicating that observation of a matching action facilitated subsequent execution. Interestingly, observation of a robot hand and arm moving to grasp the objects, or of a human actor who grasped the object blindfolded (so the movement kinematics would not differ for small and large objects), did not prime subsequent movements to small and large stimuli. Castiello et al. (2002) concluded that observation of human hand action, with kinematics tuned to the target, facilitates the later execution of human hand action.

There are several interesting questions that arise from this work. For example, in Castiello et al.'s study, the prime action was always valid on at least 50% of trials. It is possible that this encouraged participants to actively anticipate the subsequent action they would make based on the size of the object and the kinematics of the action they had just seen. Indeed, Castiello et al. (2002) not only found effects of validity on the prime trial (trial n), but also of the validity preceding the trial (trial $n-1$). The effects of a valid prime on trial n were particularly evident when the prime on trial $n-1$ was valid too. This is

consistent with an expectancy being generated according to the learning experience on the prior trial. In the present study, we repeated Castiello et al.'s (2002) study, but this time used valid primes on a minority (20%) of the trials. Thus, the most likely event was that a small object was followed by a large target object (and vice versa). Under these circumstances, participants ought to anticipate a response based on the alternative action to the one they observed. However, if the priming effect occurs relatively automatically, then observation of a valid prime action ought still to facilitate performance.

A second issue examined here was whether vision of a valid prime object alone was sufficient to facilitate action (at least in the context of a study where participants made actions on every trial). There are several studies now demonstrating that actions can be primed merely by observation of objects. For example, Tucker and Ellis (1998; see also Ellis & Tucker 2001) have found that right and left hand button presses are influenced by whether the handle of an object faces right or left, in a task where participants have to decide whether the object is upright or vertical by pressing right or left buttons. It is possible here that responses could be facilitated merely by observation of the object, on a prime trial. In Castiello et al.'s (2002) study, priming was not found when there was an inappropriate action (e.g., with the robot hand and arm), even though the appropriate object would have been observed. However, that could have been because the inappropriate action was activated by the observed kinematics of the actor and not because vision of the object alone was ineffective. Note though that if we find a positive effect of object vision, this would contradict some of the results on the characteristics of the mirror neuron system in the monkey, where both action and object have to be present

to ‘drive’ the cells (Gallese et al., 1996). We return to this point in the General Discussion.

Method

Participants

Sixteen participants took part in this experiment. They were between the ages of 17 and 25 years old and associated with the University of Birmingham. All had normal or corrected-to-normal vision and were naïve to the purpose of the study. They were paid for their participation.

Apparatus and material

Actions were measured using a dual-camera, MacReflex infrared 3D motion analysis tracking system (50HZ). Prior to experimentation, the system was calibrated using a seven-marker frame. The MacReflex software, with prior knowledge of the three-dimensional co-ordinates of six markers relative to the seventh (on the frame), determines the three-dimensional position of each camera. Infra red reflective markers (1cm diameter) were attached to the nail of each participant’s index finger and thumb and a

further marker was attached to the participant's wrist (on the same side as the thumb). Markers were fastened using double-sided tape. The wrist marker was used to determine the speed of action and the finger and thumb markers were used to determine the grasp aperture. Movement kinematics were analysed off-line using Microsoft Excel. Movement onset was taken as the time when the velocity of the wrist action exceeded 50mm/sec for three consecutive trials. The end of movement was determined by the velocity of the wrist action decreasing under 50mm/sec for three consecutive trials.

Reach and grasp actions were made to a flat-based round object that was either small (diameter of 4.5 cm) or large (diameter of 7 cm). Participants sat in the middle of a table. Before each trial, participants held a starting reference marker (diameter of 2cm) placed on the mid-sagittal axis, 5cm from the table edge. The target object was placed 30cm further along the mid-sagittal axis. A second starting reference marker (diameter of 2cm) was positioned at a right angle to the left of the target object to be used by the experimenter. It was also placed 30cm away from the target object. See Figure 1 for an illustration of the apparatus.

The vision of the participants was controlled using Plato-spectacles (Plato Technologies Inc.). The lenses were filled with liquid crystal, which was opaque unless cleared by an electric charge. The change from opaque to clear took 1ms and the change from clear to opaque took 3-5ms.

Design and procedure

The experiment involved two groups of participants. The first eight participants all observed actions directed to an object and then had to execute an action to a subsequent object. The latter eight participants either observed an action directed to an object or just observed the object (without an action), prior to executing an action to a subsequent target.

In both experiments, the trial began by the participant holding onto the starting reference with their index finger and thumb, with the Plato Spectacles opaque. Following the target object placement, the spectacles became clear for 3000ms. In this time participants either watched the experimenter making an action to the target object or just observed the target object (i.e., no action was made by the experimenter). After this, the Plato Spectacles become opaque for 3000ms. In this time, the target object could be changed. The Plato Spectacles subsequently cleared for 3000ms and the participant had to execute an action to the target object.

There were two types of trial. One was a valid trial, when the participant observed and acted to an object that was used for the prime event. There were also invalid trials, when the observation and action involved different sized objects. Valid prime trials were presented on 20% of occasions and the invalid prime on 80% of occasions. The first eight participants performed 200 and the second eight participants, 400 trials, randomised for trial type.

Data Analysis

The independent variables were prime validity (valid vs. invalid), the nature of the preceding trial (a valid prime trial vs. an invalid prime trial) and object size (small vs. large). In the main analysis we consider the data of the 16 participants who observed and then executed an action. In a later analysis we consider differences in performance as a function of whether just the object was observed or the object plus an action. This analysis was conducted on eight participants (see Participants section).

The dependent measures involved both reach components of action (movement time (ms), time to peak velocity (ms) and time after peak velocity (ms)) and grasp components (peak grasp aperture (mm) and time to peak grasp aperture (ms)) and time after peak grasp aperture (ms). These were analysed using repeated measures ANOVAs.

Figure 1 about here

Results

Observation of object + action

The results for the sixteen participants who observed both the object and the action on the prime trial are reported first. The dependent measures for the reach and grasp components of the actions are reported separately. There was a trend for movement initiation time to be slower on valid relative to invalid trials, but this was not reliable ($F[1, 15] = 3.4, p = 0.09$). Initiation times were slower however if the preceding trial was valid ($F[1, 15] = 5.54, p < 0.05$). There were no other reliable effects.

Reach component

The analysis of movement time showed reliable effects of prime validity ($F[1, 15] = 9.0, p < 0.01$) and target size ($F[1, 15] = 4.6, p < 0.05$). Movement time was less following valid prime events than following invalid prime events, and it was longer for actions to the small relative to the large objects. There was no effect of the preceding trial ($F[1, 15] = 1.7, p = 0.22$) and no reliable interactions.

There were also reliable main effects of prime validity ($F[1, 15] = 25.9, p < 0.0001$) and the preceding trial ($F[1, 15] = 6.5, p < 0.05$) on the time to peak velocity. A valid prime reduced the time to peak velocity, and this effect was further reduced if the preceding trial was valid. There was no effect of target size ($F[1, 15] < 1.0, p = n.s.$). There was one reliable interaction between prime validity and the preceding trial ($F[1,$

15] = 4.8, $p < 0.05$). Valid prime trials reduced the time to peak velocity irrespective of whether the preceding trial was valid or invalid ($F[1, 15] = 33.5$, $p < 0.0001$ and $F[1, 15] = 7.2$, $p < 0.05$ respectively). Valid prime trials (n) preceded by a valid prime trial (n-1) further reduced the time to peak velocity ($F[1, 15] = 13.6$, $p < 0.005$), whereas invalid prime trials (n) showed no change by the preceding trial (n-1) ($F[1, 15] < 1.0$, $p = \text{n.s.}$).

Analysis of the time after peak velocity showed no reliable main effects or interactions. See Figure 2 for a visual presentation of these data.

Grasp component

The analysis of peak grasp aperture showed no reliable effects of prime validity ($F[1, 15] < 1.0$, $p = \text{n.s.}$) or the preceding trial ($F[1, 15] = 1.3$, $p = 0.27$), but there was an effect of target size ($F[1, 15] = 141.9$, $p < 0.0001$). Peak grasp aperture was wider for the larger objects. There were no reliable interactions.

The time to peak grasp aperture, however, did show reliable effects of prime validity ($F[1, 15] = 9.9$, $p < 0.01$), the preceding trial ($F[1, 15] = 9.0$, $p < 0.01$) and object size ($F[1, 15] = 14.1$, $p < 0.005$). The time to peak grasp aperture was reduced on valid relative to invalid trials, on trials preceded by a valid prime event and for larger objects. There were no interactions.

Analysis of the time taken after peak grasp aperture showed no reliable effects of prime validity ($F[1, 15] < 1.0$, $p = \text{n.s.}$) or the preceding trial ($F[1, 15] = 2.9$, $p = 0.11$). However, there was a reliable effect of object size ($F[1, 15] = 30.3$, $p < 0.0001$). There was an increase in the time after peak grasp aperture for smaller objects (see Figure 2)

Figures 2 about here

Observation of action vs. object alone

Data are reported for the dependent variables found reliable in the overall analysis for action observation.

Reach component

The analysis of movement time showed a reliable main effect of object size ($F[1, 7] = 8.9, p < 0.05$), showing prolonged actions to the small relative to the large objects. There were no other main effects (observation $F[1, 7] < 1.0, p = \text{n.s.}$; prime validity $F[1, 7] = 2.1, p = 0.19$; preceding trial $F[1, 7] < 1.0, p = \text{n.s.}$). There was one reliable interaction between the observation condition and object size ($F[1, 7] = 7.1, p < 0.05$). When just the object was observed alone, there was no effect of object size ($F[1, 7] < 1.0, p = \text{n.s.}$), whereas observation of the object with an action showed longer actions to the small objects ($F[1, 7] = 21.3, p < 0.005$).

There were no overall effects on the time to peak velocity (observation $F[1, 7] = 1.1, p = 0.33$; prime validity $F[1, 7] = 4.2, p = 0.08$; preceding trial $F[1, 7] < 1.0, p = \text{n.s.}$; object size $F[1, 7] < 1.0, p = \text{n.s.}$). There was one reliable interaction between the preceding trial and object size for the time to peak velocity ($F[1, 7] = 5.7, p < 0.05$). There was no reliable effect of object size when the preceding trial was invalid ($F[1, 7] <$

1.0, $p = \text{n.s.}$), whereas time to peak velocity was less for smaller objects when the preceding trial was valid ($F[1, 7] = 5.7, p < 0.05$). These data are presented in Figure 3.

Time to peak grasp aperture

There was a reliable main effect of prime validity ($F[1, 7] = 7.2, p < 0.05$); actions had a shorter time to peak grasp aperture following a valid than an invalid prime. There were no reliable effects of observing an action relative to observing the object alone ($F[1, 7] = 2.6, p = 0.15$). There were also no effects of the validity of the preceding trial ($F[1, 7] < 1.0, p = \text{n.s.}$) or object size ($F[1, 7] = 4.6, p = 0.07$). There were no interactions. The results are shown in Figure 3.

Figure 3 about here

Discussion

Like Castiello et al. (2002), we found a reliable priming effect from the prior observation trial on the kinematics of reaching and grasping a target object. In particular, we found that the reach component of the action was faster (e.g., time to peak velocity) following a valid relative to an invalid prime. There were no reliable effects of the prime on movement initiation time, so the effect appears to arise from more efficient programming of the action, rather than speeding the start of the movement. Also similarly to Castiello et al. (2002), this priming effect tended to be larger when the preceding trial was valid (for measures of the time to reach peak velocity, priming was particularly effective following a prior valid prime trial; for the measure of movement time there was less effect of the prior trial). Thus, priming in reaching and grasping tasks is sensitive to the history of performance. The priming effect is present only when the motor representation of the observed action is subsequently used by the observer to execute the same action. This is consistent with observed actions being represented in neural systems subsequently involved in the execution of actions. Prior activation of this observation – execution system is revealed in the effects on the subsequent kinematics of action. These data occurred even though valid primes were low probability events in the study. This suggests that priming of the reach components of action occurred automatically and that any effects were not the result of conscious expectancies on the part of the participants¹. Interestingly, effects arose not only from the immediate priming event, but also according

¹ In the current results, participants would have expected an invalid trial. In Castiello et al. (2002), participants expected a valid trial. However, in both cases, valid prime trials improved the reach kinematics of actions.

to whether the preceding trial was valid. Temporal components of reaching actions were reduced particularly when both the current and the preceding trial were valid. This again replicates the data from Castiello et al. (2002). It is interesting that this effect occurred even though valid primes were low probability events. Rather than it reflecting an explicit instruction on the part of the participants, the visuo-motor action system seems implicitly tuned to priming events if they are valid (e.g., if observed is reinforced by the subsequent action).

In contrast to the effects on the reach component of action, we failed to find priming on the grasp component (the only effect was on the time to peak grasp aperture, a result that may reflect changes in the reach rather than the grasp component). Importantly, there was no hint of a priming effect on the peak grasp aperture. Castiello et al. (2002) reported effects on the peak grasp aperture. This difference between the two sets of data suggests that the grasp components of action may be influenced by conscious expectancies, and so only primed when the first action has a relatively high probability of matching the subsequent action to the target. Prior experimental and neuropsychological studies of upper limb movements have demonstrated dissociations between the reach and the grasp components of action (see Jeannerod, 1997, for an overview). The present results add to this, by indicating that reach and grasp components of action are differentially sensitive to low probability priming. This could be due to a number of factors. For example, it may be that only the neural system controlling reaching operates in a manner akin to mirror neurons, being primed by observation for subsequent action. Alternatively, the difference may reflect contrasting constraints of the environment on the various components of action. Prior work on the neuropsychology of action has indicated

that simple reaching and grasping actions are controlled by a dorsal stream in the brain (e.g., Milner and Goodale, 1995; Rossetti and Pisella, 2002). This system directs fast, immediate action to environment stimuli. Perhaps the strongest evidence for this has come from agnosic patients with damage to ventral regions of cortex that mediate object recognition. Despite their impaired recognition, such patients appear to show normal immediate reaching and grasping. Most typically, grasp actions are reported in such studies, and it may be that the grasp components of action in particular are controlled on-line through the dorsal stream. Indeed, damage to the dorsal cortex can impair the grasp more than the reach component of action in patients with optic ataxia (Goodale et al., 1994; Milner & Dijkerman, 2001; Milner et al. 2001). It follows that the grasp components of action may be somewhat robust to priming, unless there is a relatively strong top-down influence (e.g., with relatively frequent valid primes).

We also extended Castiello et al.'s (2002) study of action priming by having some participants, on some occasions, observe an object alone as the priming event. Somewhat surprisingly², we found that observation of the object alone was as effective as observing an appropriate action to an object: both primed the subsequent reach to the target. This result is important because it contrasts with the properties of mirror neurons in the monkey, as reported by Gallese et al. (1996). Similarly, Fadiga et al. (1995) showed that motor evoked potential (MEP) activity was unaffected from the presentation of visual objects when stimulating the motor cortex with TMS. In a recent paper, Gallese et al. (2002) report the properties of 236 neurons in the inferior parietal cortex. Out of these

² Note that each participant received 80 valid prime trials (40 observation of an action made to the object and 40 observation of the object without action). Therefore, the lack of interaction was not due to a lack of trials.

neurons, 61 responded to observation of actions (43/61 responded in a “mirror” type fashion). More neurons were responsive just to when the monkey made an action (130 neurons). Of these, 17 responded just to the visual stimuli. Apparently, presentation of the object alone has no effect on neurons associated with movement observation.

However, the object to be acted toward is important when executing an action and has an appropriate neural representation (see also Sakata and Taira, 1994). From this contrast between physiological data on mirror neurons and the behavioural data, we may suggest that the mirror – neuron system, may not be the only mediator of action priming³.

Another suggestion might be that the presentation of the object in the observation stage of the experiment, afforded action towards it, and primed components of the subsequent reaching action (Gibson, 1966). This would fit with the evidence for compatibility effects based on the left – right orientations of objects, even though left – right orientation is irrelevant to the task (Ellis & Tucker, 2001; Tucker & Ellis, 1998, 2002). It is possible that the object represents the goal of the action. Prior observation of the object may prime the goal representation, facilitating components of the subsequent action. This last argument is consistent with developmental research in which children have been asked to imitate actions performed by an experimenter. Bekkering et al. (2000) asked children to imitate complex actions performed by the experimenter using either the left or right hands. They found that the children imitated the goal of the action (reaching to the correct target) but they made frequent mistakes by using the incorrect hand.

³ The mirror – neuron system may account for some of the action priming as Castiello et al., (2002) showed that actions were not primed when the observed actions had the same movement kinematics for small and large objects (robot and blind actors). Here, observation of an inappropriate reach to a valid prime object produced no subsequent improvement in response. Therefore, observation of the inappropriate reach dispelled the priming effect from the object.

Bekkering et al. (2000) suggest that imitation of action is modulated by the goal of the task and not by mimicking the precise movements to produce the goal. In the present study, priming the goal of the action, through observation of the subsequent target in a valid priming event, may be sufficient to alter the later reaching action. Of course, in everyday life it may be that any affordance – based system would be co-ordinated with a mirror – neuron type system. For example, a mirror – neuron system could play a role in monitoring action, linking an ongoing action to a goal for error correction (see Wolpert and Kawato, 1998; Wolpert et al. 1998; Imamizu et al., 2000; Blakemore et al. 2001; Blakemore and Decety, 2001). The goal for this monitoring system may be established through an affordance – based system.

A further possibility is that priming here was determined not only by observation of the object, but also by joint attention to the object by the experimenter and the participant. Jellema, Baker, Wicker and Perrett (2000) have recently described a population of cells in the anterior part of the superior temporal sulcus (STS) in the macaque. These cells were selective for reaching actions when attention of an actor looked at the target of a subsequent action. Thus, information about another person's gaze to an object may be integrated with the processes underlying the planning and execution of arm movements, even without the need to see the action being performed. This requires further research before we can assess whether joint attention is important here.

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Figure captions

Figure 1: Experiment set-up and apparatus.

Figure 2: Results for the reach and grasp components. Means are shown for (a) movement time (ms), (b) time to peak velocity (ms), (c) time taken after peak velocity (ms), (d) peak grasp aperture (mm), (e) time to peak grasp aperture (ms), and (f) time after peak grasp aperture (ms). The data are shown for small and large objects and the validity of the prime event.

Figure 3: The effects of observing an object + an action vs. observing the object alone. Means are shown for (a) time to peak velocity (ms), and (b) time to peak grasp aperture (ms). The data are broken down as a function of: object size, prime validity and whether the object + action was observed or the object alone.

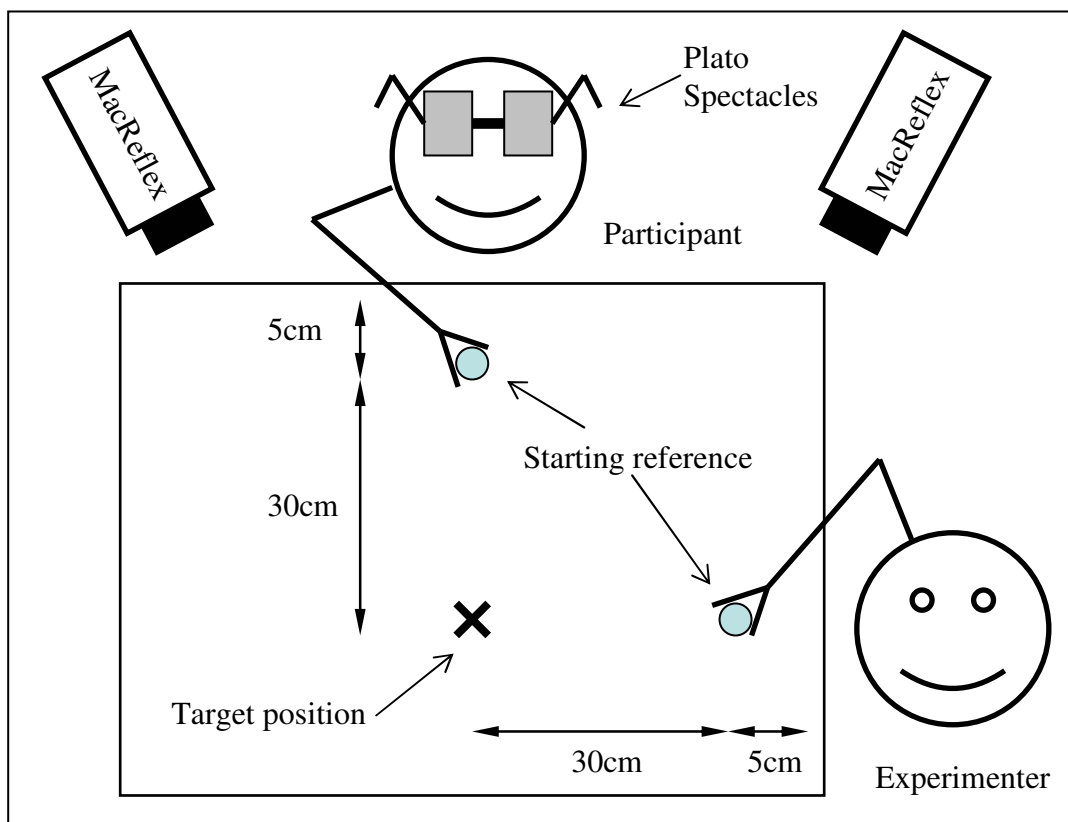


Figure 1

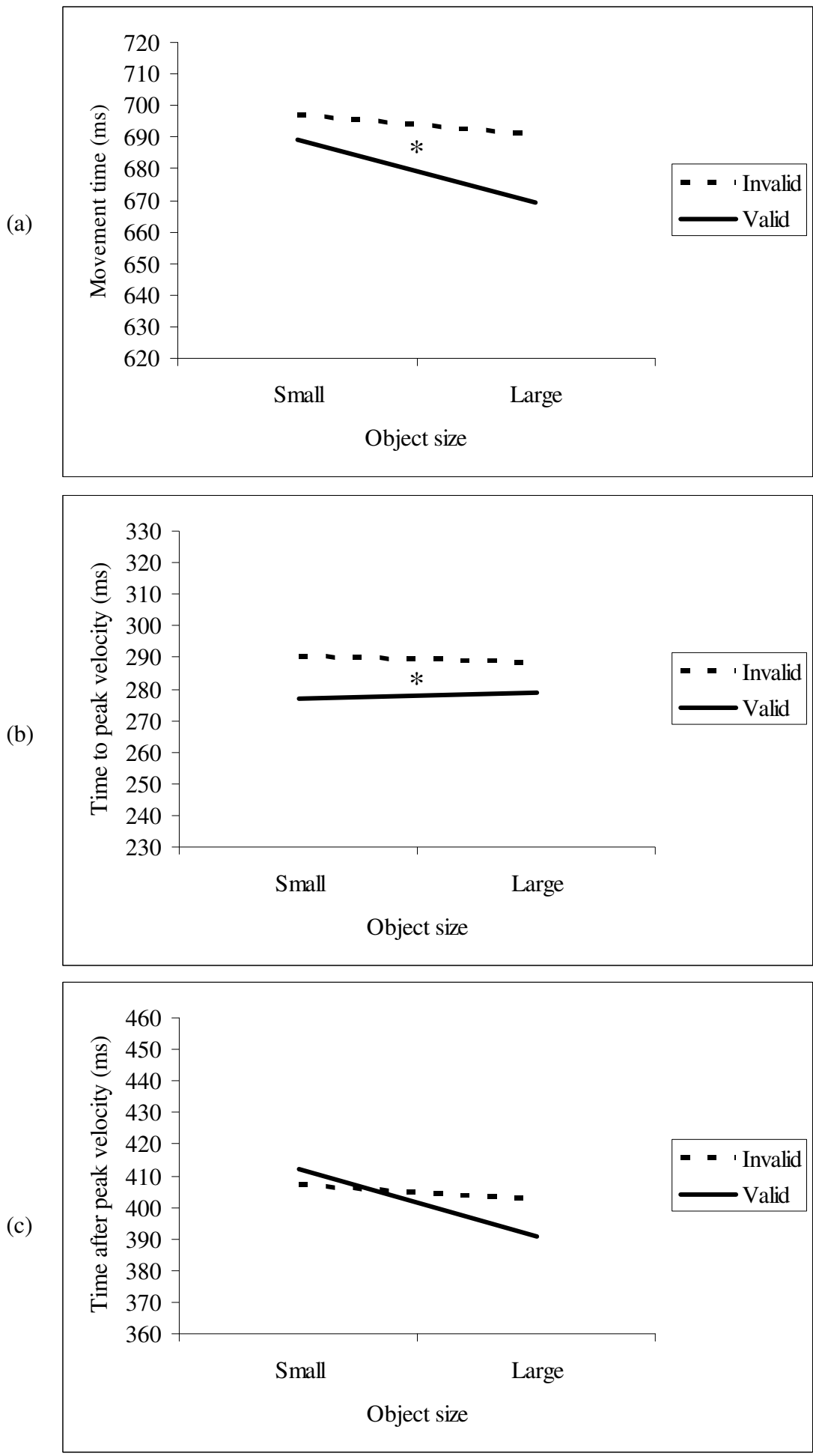


Figure 2

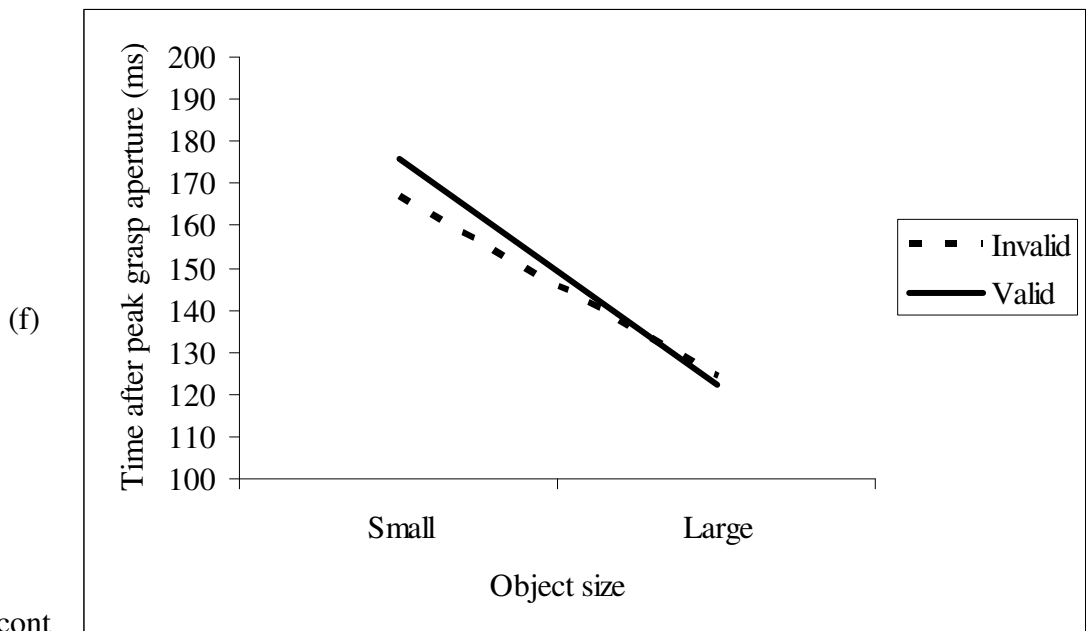
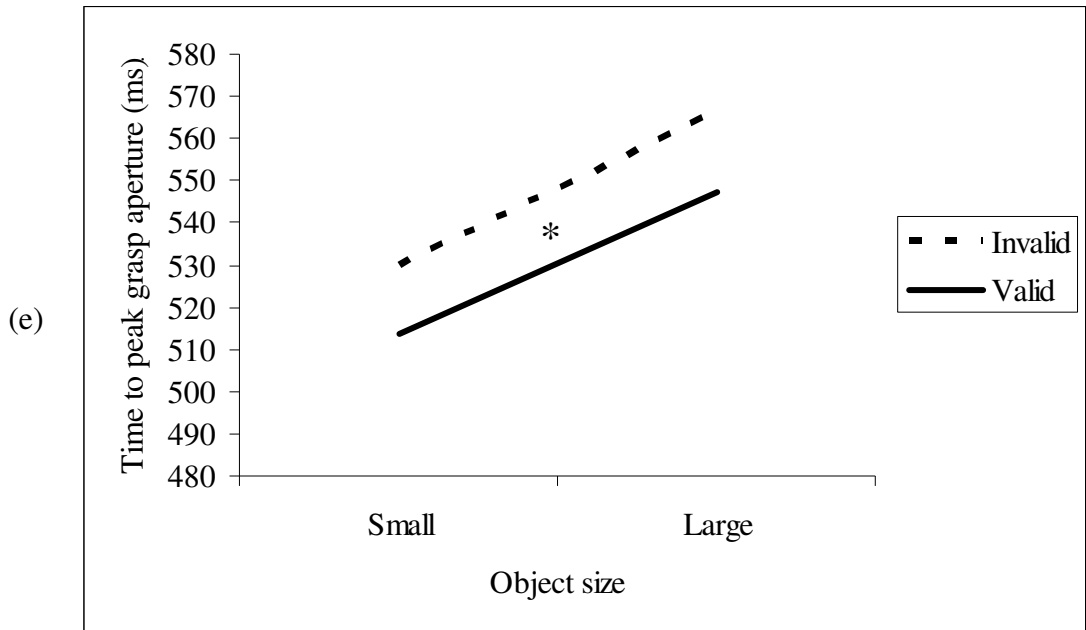
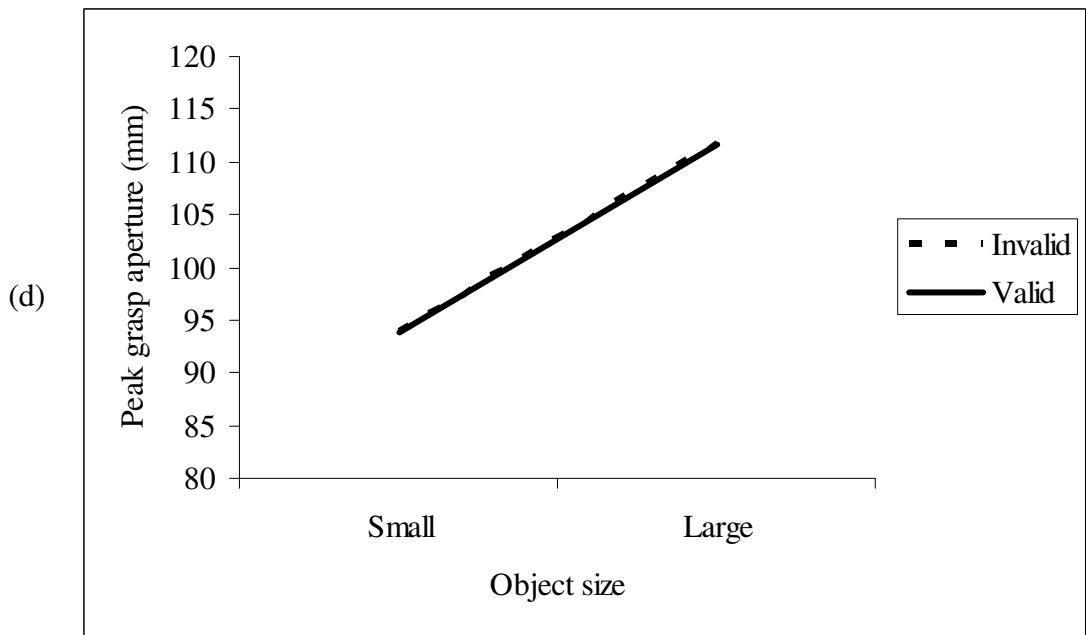
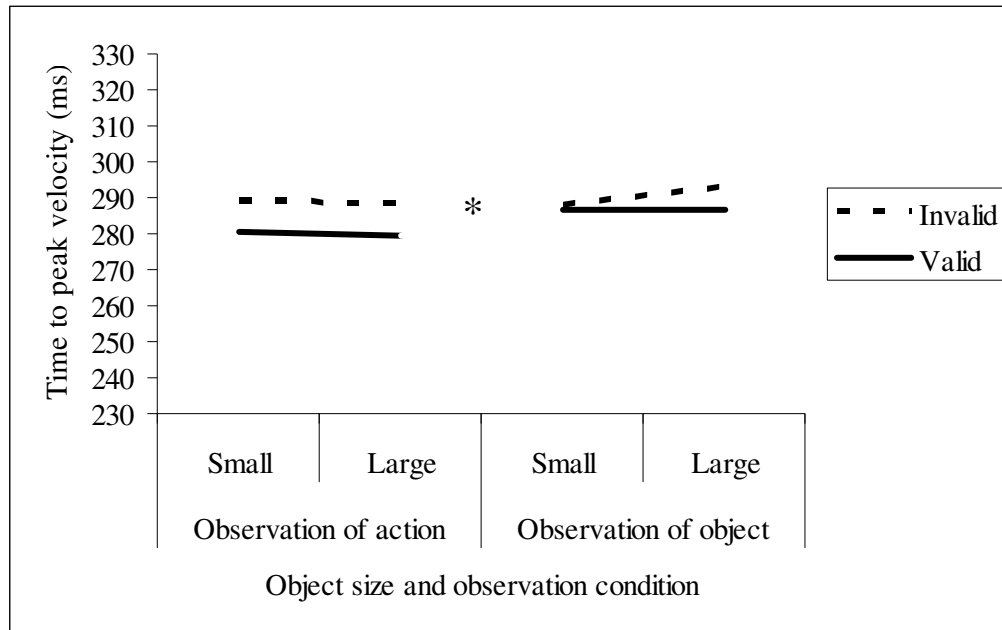


Figure 2 cont

(a)



(b)

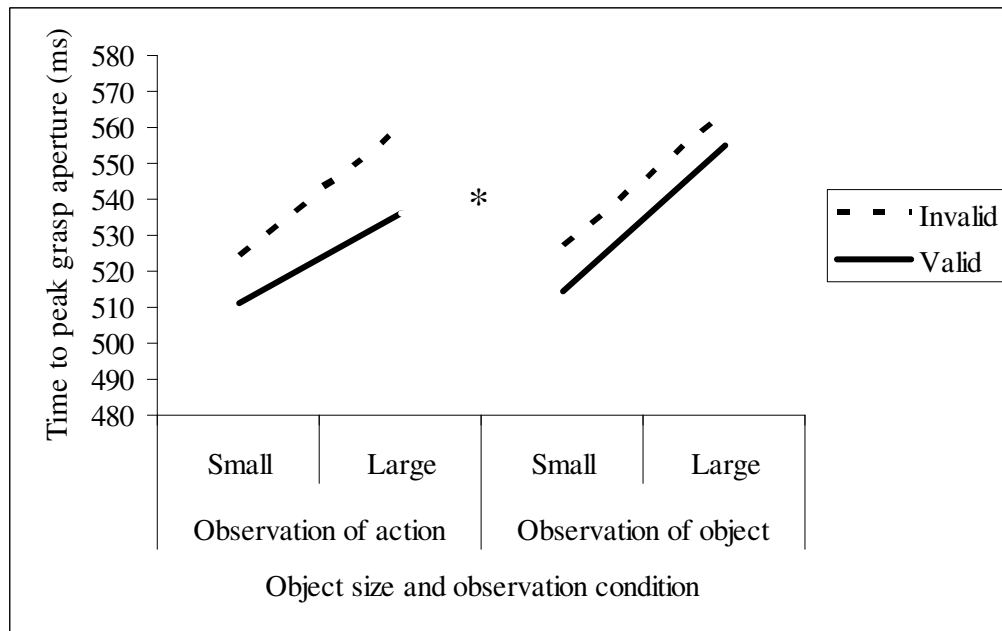


Figure 3