Automatic Recruitment of the Motor System by Undetected Graspable Objects: A Motor-evoked Potential Study

Nicolas A. McNair, Ashleigh D. Behrens, and Irina M. Harris

Abstract

Previous behavioral and neuroimaging studies have suggested that the motor properties associated with graspable objects may be automatically accessed when people passively view these objects. We directly tested this by measuring the excitability of the motor pathway when participants viewed pictures of graspable objects that were presented during the attentional blink (AB), when items frequently go undetected. Participants had to identify two briefly presented objects separated by either a short or long SOA. Motor-evoked potentials were measured from the right hand in response to a single TMS pulse delivered over the left primary motor cortex 250 msec after the onset of the second target. Behavioral results showed poorer identification of objects at short SOA compared with long SOA, consistent with an AB, which did not differ between graspable and non-graspable objects. However, motor-evoked potentials measured during the AB were significantly higher for graspable objects than for nongraspable objects, irrespective of whether the object was successfully identified or undetected. This provides direct evidence that the motor system is automatically activated during visual processing of objects that afford a motor action.

INTRODUCTION

A large body of research suggests that viewing objects associated with a grasping action engages the motor system, even when the observer is not preparing to grasp the object. One line of evidence for this comes from studies that have measured response compatibility effects. These experiments have demonstrated that manual responses (e.g., button presses) to graspable objects are made faster when the handle of the pictured object is oriented toward the responding hand (Tucker & Ellis, 1998) or when the manual responses performed are compatible with the manner in which the object is typically grasped (Ellis, Tucker, Symes, & Vainio, 2007; Vainio, Ellis, Tucker, & Symes, 2006; Tucker & Ellis, 2001). Other studies have also shown that object attributes that afford particular actions could prime the preparation of a motor response, other studies have also shown that motor-related object features can influence object identification, and do so even when the observer is passively viewing the objects without preparing to make a motor response. For example, objects that afford a particular grasp facilitate identification of subsequently presented objects that are associated with a similar grasp (Harris, Murray, Hayward, O’Callaghan, & Andrews, 2012; McNair & Harris, 2012; Helbig, Graf, & Kiefer, 2006). Taken together, this evidence suggests that the mere observation of graspable objects or tools results in increased activation throughout the frontoparietal motor network, including the dorsal and ventral premotor cortex, SMA, primary motor cortex, inferior parietal lobule, and intraparietal sulcus, particularly in the left hemisphere (Fabbri, Stubbs, Cusack, & Culham, 2016; Menz, Blangero, Kunze, & Binkofski, 2010; Vingerhoets, 2008; Creem-Regehr & Lee, 2005; Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004; Grèzes & Decety, 2002; Chao & Martin, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997). Activation within this network is elicited both when participants view tools and when they engage in motor imagery related to such objects (Grèzes & Decety, 2002), and this activity has been shown to correlate with the magnitude of the affordance-based compatibility effect (Grèzes, Tucker, Armony, Ellis, & Passingham, 2005).

Even more direct evidence for a link between the motor system and object perception is provided by studies that measured motor-evoked potentials (MEPs) elicited by TMS of the primary motor cortex during the perception of graspable objects. The amplitude of an MEP indexes the excitability of the corticospinal pathway...
at the point in time when the TMS pulse occurs. Using this technique, Makris, Hadar, and Yarrow (2011) found that MEPs measured from the first dorsal interosseous (FDI) muscle, which controls abduction of the index finger, were larger when participants viewed objects that were normally grasped using a precision grip (which more specifically involves the FDI muscle) as opposed to a power grip (which involves the entire hand). Intriguingly, the magnitude of MEPs elicited while viewing a graspable object is modulated by violations of one’s ability to interact with that object. For instance, MEPs elicited in the right hand were found to be larger when participants viewed graspable objects with handles oriented toward that hand, compared with those oriented toward the left hand, but this advantage disappeared when the same objects were depicted with broken handles (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009). Furthermore, modulation of MEP amplitude elicited by graspable objects was only observed when these objects were depicted as being in reachable space (Cardellicchio, Sinigaglia, & Costantini, 2011). These findings, therefore, indicate that the excitability of the motor pathway is sensitive to the object’s perceived “graspability” and could be used as a direct measure of the engagement of the motor system during visual perception of objects. A further advantage of this method of examining motor system engagement in a visual processing task is that, unlike in fMRI or behavioral studies, the timing of the TMS pulse administered to the primary motor cortex gives precise information about the time window in which the excitability of the motor system is modulated by a perceived object.

An outstanding question, which motivates this study, is whether the motor system is automatically engaged by the perception of graspable objects or whether it is only recruited when observers engage in deliberate motor imagery or prepare an actual motor response. In the context of compatibility-based motor priming effects, a recent study has suggested that such effects only arise when participants explicitly attend to the spatial configuration of the objects and, most critically, only if they imagine picking up the object when making their decision (Yu, Abrams, & Zacks, 2014). Murphy, van Velzen, and de Fockert (2012) have additionally shown that compatibility effects are abolished under high perceptual load, when insufficient attention is available for distractor processing. This suggests that processing action affordances requires attention. In contrast, others have claimed that compatibility effects can be observed even when the graspable objects fall at unattended spatial locations (Makris, Hadar, & Yarrow, 2013) or are rendered invisible through brief masked exposure (Pappas & Mack, 2008; Tucker & Ellis, 2004). Given that motor imagery is improbable under such conditions, such findings suggest that the motor compatibility effects arise automatically (i.e., nonstrategically) and perhaps even without the need for conscious awareness of the stimulus.

With regard to object identification, some studies have manipulated the visibility of objects through continuous flash suppression (Tsuchiya & Koch, 2005) and have reported categorical priming effects from unseen tool objects (Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008), which the authors interpreted as evidence for unconscious recruitment of dorsal visual stream (Fang & He, 2005). However, it is important to note that the study by Fang and He (2005) did not report any specific activations in the motor cortex itself and more recent studies have failed to find evidence of any dorsal stream activation in response to suppressed pictures of tools (Ludwig, Kathmann, Sterzer, & Hesselmann, 2015). Thus, at present, there is no clear evidence of motor system activation by tools that are suppressed from conscious awareness. Furthermore, the priming effects demonstrated in these continuous flash suppression studies may be mediated by coarse shape features that correlate with the category of “tools,” such as elongation, rather than indicating specific activation of object identity (Almeida et al., 2014; Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012).

In this study, we used MEPs elicited through TMS of the primary motor cortex to directly probe the underlying excitability of the motor pathway and asked whether this is potentiated by the mere presence of a graspable object that fails to attain full identification, or even conscious awareness. We used an attentional blink (AB) paradigm to limit the conscious identification of the objects of interest. In this paradigm, two visual targets are presented sequentially in the same spatial location, under conditions of rapid serial visual presentation (RSVP; 10–12 items/sec). Under these conditions, a single target presented in an RSVP stream of distractors is easily detected. But when participants have to identify two targets in close succession, detection of the second target (T2) is impaired when it follows the first target (T1) with an SOA of ~200–600 msec (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992). It is widely accepted that the difficulty in reporting T2 arises after the initial perceptual processing of the targets, at a processing stage that allows consolidation of T2 in a consciously accessible form (Olivers & Meeter, 2008; Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Chun & Potter, 1995; Raymond et al., 1992). Indeed, there is very good evidence that all items presented in an RSVP stream are processed to relatively high perceptual and conceptual levels, as demonstrated by their ability to prime other, related items (Harris, Benito, & Dux, 2010; Harris & Little, 2010; Pappas & Mack, 2008; Vogel, Luck, & Shapiro, 1998; Maki, Frigen, & Paulson, 1997; Luck, Vogel, & Shapiro, 1996). Neural evidence supports this, showing intact processing of target stimuli in the ventral visual stream associated with perceptual analysis of the stimuli but disrupted activity associated with attentional selection and working memory encoding (Sergent, Baillet, & Dehaene, 2005; Marois, Yi, & Chun, 2004; Vogel et al., 1998). Particularly
pertinent to the present investigation, two recent studies have shown facilitated processing of items presented during the AB that were related to the first target through a joint action (McNair & Harris, 2014; Adamo & Ferber, 2009), and another found that response compatibility effects could be induced by an object presented during the AB (Pappas & Mack, 2008). Together, these studies suggest that motor associations can be processed for “blinking” items. Thus, the AB provides an ideal paradigm to test whether the motor system is automatically engaged in the presence of a graspable object when the conscious detection and identification of the objects is severely limited and there is no motor response associated with it.

We recorded MEPs from the right FDI muscle evoked by TMS pulses delivered to the corresponding hand area of the left primary motor cortex, while participants identified pictures of objects. In a preliminary experiment (Experiment 1), we tested whether graspable objects evoke larger MEPs than nongraspable objects when presented in isolation at the fast temporal rates used in RSVP paradigms. It is important to establish this because previous studies that demonstrated modulation of MEPs by graspable objects used relatively long stimulus exposures (e.g., Buccino et al., 2009) and there is some evidence that the offset of a graspable object can result in inhibition of a motor response (Vainio, Hammaren, Hausen, Rekolainen, & Riskila, 2011; Vainio, 2009), which may affect the MEP. Experiments 2 and 3 then used an AB paradigm and measured MEP modulation by the second target object (T2), which could be either a graspable or nongraspable object. In Experiment 2, the first target (T1) was always a nongraspable object, whereas in Experiment 3, both T1 and T2 could be either graspable or nongraspable (fully crossed) to test for contextual effects. If the motor system is automatically engaged by the perception of graspable objects, we should continue to see potentiation of MEPs by such objects even when their conscious detection is disrupted by the AB (i.e., when it follows T1 with a short SOA), and this potentiation should be similar to that observed when the object is not affected by the AB.

METHODS
Participants
Right-handed participants were recruited from the University of Sydney undergraduate psychology pool in exchange for partial course credit. Twenty-two (13 women; mean age = 22 years, range = 18–47) participated in Experiment 1, another 22 (11 women; mean age = 21 years, range = 18–31) took part in Experiment 2, and a further 22 (17 women; mean age = 19 years, range = 17–21) took part in Experiment 3. The sample size was based on our prior experience with AB experiments, where 20–24 participants are sufficient to see any effects of different object manipulations (e.g., McNair & Harris, 2014; Harris et al., 2010). Participants completed a TMS safety screening and provided their informed consent in writing before commencing the experiment. All experimental procedures were approved by the Human Research Ethics Committee of the University of Sydney.

Apparatus and Stimuli
The experiment was run on a PC using PsychoPy software (Peirce, 2007) to control stimulus presentation, triggering of TMS, and response collection. Images were displayed on a 17-in. BENQ CRT monitor (1280 × 1024 pixel resolution, 60 Hz refresh rate) at a viewing distance of ~114 cm.

Stimuli were color images obtained from a photo-object database (Hemera, Inc., Montreal, QC, Canada) and Google Image Search. Target stimuli used in both Experiment 1 and Experiment 2 consisted of 20 graspable and 20 nongraspable objects (see Appendix 1). In Experiment 3, this was reduced to 15 graspable and 15 nongraspable objects to accommodate the increase in the number of conditions. The graspable objects were selected on the basis of having an identifiable handle or elongated shape and were associated with either whole-hand grasps (e.g., hammer) or with precision grasps (e.g., pen). These objects were oriented to have their handles pointing toward the right hand. An additional 40 images of nongraspable objects were used as T1 stimuli in Experiment 2, whereas in Experiment 3 the same collection of stimuli was used for both T1 and T2. The objects subtended 3°–9° of visual angle and were presented against a light gray background. Eight square masking stimuli, 11.5° in size, were also created by superimposing small fragments of the entire set of images into patchwork-like compositions (see Figure 1).

EMG and TMS Procedures
Surface EMG traces were recorded from the FDI muscle of the right hand, using a pair of Ag/AgCl electrodes placed in a belly–tendon arrangement over the muscle along with a ground electrode placed over the ulnar styloid process of the wrist. Data from 200 msec prestimulus to 100 msec poststimulation were collected via a PowerLab 26T DAQ device (ADInstruments, Bella Vista, NSW, Australia). The EMG signal was digitized (sampling rate: 4 kHz; bandpass filter: 0.5 Hz to 2 kHz; mains filter: 50 Hz) and stored on a computer using LabChart software (Version 8, ADInstruments) for offline analysis.

TMS was administered by either a Magstim 200² (Experiments 1 and 3) or Rapid² (Experiment 2) stimulator using a 70-mm figure-eight coil (Magstim, Whitland, UK). Timing was synchronized through TTL signals from the test computer to the Magstim unit. Participants wore an elastic cap with the electrode locations corresponding to the 10/20 EEG system marked on it. The location of the
The motor cortex “hotspot” was determined starting from a spot 5 cm lateral and 1 cm anterior to Cz and moving the coil until the maximal MEP was elicited in the FDI muscle. Once this was located, pulses were delivered with the coil positioned in a posterior–anterior configuration, with the handle oriented 45° from midline. The coil was locked in position with the aid of a mechanical arm (Manfrotto, Cassola, Italy) while participants were seated comfortably with their heads kept stable using an adjustable forehead and chin rest. This ensured that any movement during the experiment was minimized and that the targeted location was maintained. Resting motor threshold (rMT) was identified as the lowest stimulation intensity capable of inducing MEPs with a minimum of 50 μV amplitude in 5 of 10 consecutive pulses (Rossini et al., 2015). Pulse intensity during the experiment was then set at 120% of rMT, with the exception of four participants with relatively high rMTs. These participants experienced physical discomfort at 120% rMT intensity, and so this was reduced to 110%. Across participants, the average stimulator intensity used was 46.5% of maximum stimulator output in Experiment 1, 63.7% in Experiment 2, and 47.9% in Experiment 3. The difference in intensity between Experiment 2 and the other two experiments is attributable to the fact that the two stimulators used have somewhat different power outputs and pulse characteristics: The Rapid² produces a biphasic waveform, whereas the Magstim 200² produces a monophasic waveform. These differ in the primary direction of the electrical current elicited at the cortical level, which in turn affects the strength of the evoked MEP (Delvendahl et al., 2014).

On each trial, a single TMS pulse was delivered at approximately 250 msec after the onset of the target stimulus (T2 in Experiments 2 and 3). This particular timing was chosen based on prior research that demonstrated modulation of neural activity in the motor areas in response to graspable objects in a time window 184–288 msec after stimulus onset (Kourtis & Vingerhoets, 2015; Mizelle & Wheaton, 2010; Petit, Pegna, Harris, & Michel, 2006). We confirmed this in a pilot experiment (N = 9) in which participants viewed the same graspable and nongraspable objects in isolation while TMS pulses were delivered at either 150 or 250 msec poststimulus. Of the two latencies, 250 msec yielded a more reliable difference in MEP amplitudes between graspable and nongraspable objects. All responses were collected with the left hand using a mouse. Participants were instructed to keep their right hand relaxed and still during the trial.

Data Analysis

Analysis of MEP data was conducted using custom software written in Python. Following standard methods in this literature (e.g., Cardellicchio et al., 2011; Labruna, Fernández-del-Olmo, & Ivry, 2011; Makris et al., 2011; Buccino et al., 2009; Duque et al., 2005), trial data were visually inspected for EMG activity before the TMS pulse, and any such trials were excluded. MEP amplitudes were then measured using peak-to-peak difference values. These were normalized for each participant by comparison to baseline MEP measurements (Experiment 1) or with respect to the individual’s grand mean (Experiments 2 and 3).
In Experiment 3, we also collected baseline MEP measurements in separate trials in which no T2 object was shown to verify whether there might be any effect of the T1 object on MEPs. Because none was apparent, we report the data normalized to each participant’s grand mean for consistency with Experiment 2 data. Statistical analyses of the normalized peak-to-peak amplitudes and behavioral data were conducted using SPSS software (Version 22, IBM, Armonk, NY) as outlined in each experiment.

**Experiment 1**

**Procedure.** All trials began with a fixation cross at the center of the screen displayed for 500–1000 msec, followed by the presentation of the target graspable or nongraspable object (see Figure 1 for an example of the trial structure). In Brief-display trials, this was displayed for 83 msec followed by a mask for a further 83 msec. In Long-display trials, the stimulus was shown for 500 msec and was not masked. Both types of trials ended with a fixation cross presented for 500 msec before the response screen was displayed. This consisted of 16 objects arranged in a 4 × 4 array and contained eight graspable and eight nongraspable objects, including the stimulus shown during the trial. Participants selected the object they had seen, with the screen remaining until a response was made. Following the response, the duration of the intertrial interval varied based on the RT such that there was always at least 5 sec between the onset of the response screen and the start of the subsequent trial. The Brief and Long trials were shown in separate blocks, with the order counterbalanced between participants. Each graspable and nongraspable object was shown twice for each display duration, resulting in 80 experimental trials per block (40 graspable and 40 nongraspable). In addition, each block began with four practice trials to accustom the participant to the trial structure and speed.

Three short baseline blocks were also presented, the first before Block 1, the second between Blocks 1 and 2, and the third following Block 2. We collected baseline MEP measurements in separate blocks, based on the findings of Labruna and colleagues (2011) that unbiased baseline measurements are best obtained between experimental blocks rather than during experimental blocks. In each baseline block, 10 MEPs were collected while the participant fixated on a cross at the center of the screen. These baseline MEPs were used to normalize the peak-to-peak amplitude of the MEPs collected during the experimental blocks. For each participant, the MEPs recorded during the first experimental block were expressed as a percentage of the average baseline MEP derived from the first and second baseline blocks. For the second experimental block, the MEPs were normalized using the average derived from the second and third baseline blocks. This was done to control for any change in overall MEP amplitude across the entire experimental session.

**Experiment 2**

**Procedure.** This experiment employed a fairly standard AB paradigm with two targets presented on each trial, separated by either a long SOA or a short SOA (see Figure 2). Each trial began with a fixation cross for 500–1000 msec. This was followed by a target object (T1) presented for 83 msec and then a mask, also presented for 83 msec. On all trials, T1 was a nongraspable object. On Short SOA trials, the second target (T2) occurred immediately following the offset of the T1 mask (T1 – T2 SOA: 167 msec). On Long SOA trials, following the T1 mask a fixation cross was presented for 583 msec before displaying T2, resulting in a T1 – T2 SOA of 750 msec. The T2 stimulus was presented for 83 msec and was immediately followed by an 83-msec mask. A fixation cross then followed for 500 msec, before the T1 response screen was displayed. This consisted of a 4 × 4 array of objects composed of the T1 stimulus and 15 foils drawn randomly from the other T1 stimuli. After participants made their response, the T2 response screen was displayed, which also consisted of a 4 × 4 array of objects. Of these, eight were graspable and eight were nongraspable objects, including the T2 stimulus. Both responses were made with the mouse using the left hand. After the T2 response, there was a variable ITI that ensured at least 5 sec elapsed between the onset of the response screens and the start of the next trial. This type of “skeletal” RSVP, which does not contain any distractors, is a variation of the more standard AB paradigm in which targets are embedded within a stream of distractors, but it still produces a reliable AB (Ward, Duncan, & Shapiro, 1997). Each type of T2 object (graspable, nongraspable) was presented twice at each SOA (Short, Long), resulting in 40 trials per condition (Graspable-Short SOA, Graspable-Long SOA, Nongraspable-Short SOA, Nongraspable-Long SOA; 160 experimental trials total).

In addition to the experimental trials, participants completed four practice trials before commencing the experiment proper. Overall, the session lasted approximately 1 hr, including the preliminary setting up for MEP measurement.

**Experiment 3**

**Procedure.** The procedure used in Experiment 3 was largely identical to that used in Experiment 2; however, T1 stimuli were also graspable or nongraspable objects. This resulted in eight experimental conditions: Graspable T1/Graspable T2/Short SOA (GT1GT2-Short), Graspable T1/Nongraspable T2/Short SOA (GT1NT2-Short), Nongraspable T1/Graspable T2/Short SOA (NGT1GT2-Short), Nongraspable T1/Nongraspable T2/Short SOA (NGT1NT2-Short), Graspable T1/Graspable T2/Long SOA (GT1GT2-Long), Graspable T1/Nongraspable T2/Long SOA (GT1NT2-Long), Nongraspable T1/Graspable T2/Long SOA (NGT1GT2-Long), and Nongraspable T1/Nongraspable T2/Long SOA (NGT1NT2-Long). T1 and
T2 were drawn from the same pool of stimuli with the proviso that identical stimuli were never shown either on the same trial or on consecutive trials. Because of the increase in number of conditions, we reduced the number of trials per condition from 40 to 30, by using only 15 stimuli of each type, which were each shown twice in each condition. In addition to these 240 experiment trials, a further 60 baseline trials were included, 30 at each SOA, in which a blank screen was shown in place of the T2 stimulus. All trials were randomly intermixed. Overall, the session lasted approximately 1.5 hr.

RESULTS

Experiment 1

The accuracy and MEP amplitude data were each analyzed using a 2 (Display duration) × 2 (Object type) repeated-measures ANOVA.1

Behavioral Accuracy

Participants were slightly more accurate in their identification of items displayed for a long duration (99.6%, SEM = 0.2%) than a brief duration (98.5%, SEM = 0.5%; F(1, 21) = 5.0, p = .036, ηp2 = .19). There was no difference in accuracy between graspable (99.8%, SEM = 0.3%) and nongraspable objects (99.1%, SEM = 0.3%; F(1, 21) < 1), nor any interaction between the graspability of the object and stimulus duration (F(1, 21) < 1).

MEP Amplitude

There was no main effect of Display duration on overall MEP amplitude (Long: 109.5%, SEM = 7.1%; Brief: 99.8%, SEM = 4.2%; F(1, 21) = 1.96, p = .176, ηp2 = .09). Across both display durations, graspable objects (109.4%, SEM = 5.5%) elicited significantly larger MEPs than nongraspable objects (99.9%, SEM = 4.4%; F(1, 21) = 15.0, p < .001, ηp2 = .42; see Figure 3). There was no interaction between Display duration and Object type (F(1, 21) < 1). Follow-up comparisons confirmed that MEPs were significantly larger for graspable compared with nongraspable objects both for brief displays (t(21) = 2.9, p = .006) and for long-duration displays (t(21) = 2.3, p = .035).

Figure 2. Experiments 2 and 3 trial structure (note that for display purposes the stimuli are not shown exactly to scale). In both experiments, trials began with an initial fixation cross displayed for 500–1000 msec. Then an object (T1; always nongraspable in Experiment 2, either graspable or nongraspable in Experiment 3) was presented at the center of the screen for 83 msec, followed by a backward mask for 83 msec. In the short SOA trials, this was followed immediately by another object (T2; either graspable or nongraspable) presented for 83 msec, followed by a backward mask for a further 83 msec. In the Long SOA trials, an additional fixation cross was displayed for 583 msec following the T1 mask. After a fixation cross lasting 500 msec, participants were prompted to indicate which object had appeared as T1 and then which object had appeared as T2.
The results of Experiment 1 show a clear difference in the amplitude of the MEPs elicited in the presence of graspable compared with nongraspable objects. These results corroborate previous findings of increased excitability in the motor cortex during passive viewing of graspable objects relative to nongraspable objects, when motor response preparation is not required (Cardellicchio et al., 2011; Buccino et al., 2009). Importantly, this enhancement occurred in equal measure when participants had a relatively protracted and unobstructed view of the stimulus and when the object was shown only briefly and backward masked. The accuracy of identifying graspable versus nongraspable objects did not differ, and it was close to ceiling at both display durations, although slightly better overall with long duration. Taken together, these findings indicate that the stimulus presentation parameters used in typical AB paradigms should not, in and of themselves, compromise our ability to see enhanced MEPs for graspable compared with nongraspable objects.

**Experiment 2**

**Behavioral Accuracy**

T1 and T2 accuracy data were analyzed separately using ANOVAs with SOA (Short vs. Long) and T2 type (Graspable vs. Nongraspable) as within-subject factors.

Overall, T1 accuracy was very high (96.0%, SEM = 0.7%). There was no difference between trials with a graspable (95.9%, SEM = 0.8%) or nongraspable (96.1%, SEM = 0.8%) object presented as T2 (F(1, 21) < 1). There was a marginal effect of SOA, with T1 performance suffering slightly on short-SOA (95.3%, SEM = 0.9%) compared with long-SOA trials (96.6%, SEM = 0.7%; F(1, 21) = 4.1, p = .055, $\eta^2 = .16$). There was no interaction between the T2 type and SOA (F(1, 21) < 1).

**MEP Amplitude**

In Experiment 1, MEPs recorded in the presence of object targets were always above the baseline MEPs measured without a stimulus present (i.e., there was no indication of motor inhibition for any of the objects). Given this, in this experiment we removed the no-object baseline blocks and instead used each participant’s grand mean to normalize their data. This allowed us to reduce the number of TMS pulses delivered during the experiment without a loss of important information, because we were only interested in the relative difference between graspable and nongraspable objects. The normalized peak-to-peak values were analyzed with the same ANOVA as the behavioral results, using the factors SOA (Short vs. Long) and T2 type (Graspable vs. Nongraspable). To mirror the T2 behavioral accuracy, MEPs were only included in the analysis if T1 had been correctly identified on that trial. These results are presented in Figure 4A.

Graspable objects (104.3%, SEM = 1.9%) elicited significantly larger peak-to-peak amplitudes than nongraspable objects (95.5%, SEM = 1.9%; F(1, 21) = 5.2, p = .033, $\eta^2 = .20$). The difference in overall MEP amplitude between the two SOA conditions approached significance (F(1, 21) = 3.78, p = .066, $\eta^2 = .15$), with MEPs being slightly larger at the short SOA (107.7%, SEM = 4.0%) than the long SOA (92.0%, SEM = 4.0%). Notably, there was a significant interaction between T2 type and SOA (F(1, 21) = 7.6, p = .012, $\eta^2 = .27$). MEPs were significantly larger for graspable (119.8%, SEM = 4.7%) than nongraspable (95.7%, SEM = 5.5%) objects at the Short SOA (p < .001), but this difference failed to materialize at the Long SOA (Graspable: 88.8%, SEM = 4.9%; Nongraspable: 95.2%, SEM = 5.9%; p = .383).

A second analysis examined the MEPs for targets presented at the short SOA only, dividing them according to whether T2 was correctly identified or not (i.e., “missed” targets); these data are presented in Figure 4B. Two participants were excluded from this analysis because of having too few trials in one of the conditions (<3 trials), although the results are essentially identical if these participants are retained. An ANOVA with Target detection (Correct vs. Missed) and T2 type (Graspable vs.
Nongraspable) as within-subject factors confirmed the previously found main effect of T2 type, with larger MEPs for graspable objects (118.7%, \( SEM = 6.7\% \)) than nongraspable objects (98.3%, \( SEM = 6.4\% \); \( F(1, 19) = 6.8, p = .017, \eta^2_p = .26 \)). Note that the exact values differ slightly here from the previous analysis because of the reduced number of participants and the sorting of trials into Correct and Missed categories. Importantly, MEPs did not differ in overall magnitude for missed (114.6%, \( SEM = 8.4\% \)) and correctly identified targets (102.4%, \( SEM = 5.7\% \); \( F(1, 19) = 1.5, p = .235, \eta^2_p = .07 \)), and this did not interact with T2 object type (\( F(1, 19) = 2.0, p = .172, \eta^2_p = .10 \)). Although the pattern of MEPs elicited by graspable and nongraspable objects did not differ significantly as a function of whether the item was correctly identified or not, inspection of Figure 4B suggests that the absolute size of the MEP enhancement for the graspable objects was numerically greater for correctly identified targets. This appears to be due primarily to an increase in the size of MEPs elicited by nongraspable objects on missed trials. Conversely, the size of MEPs elicited by graspable objects was comparable irrespective of whether the object had been identified correctly or not. Therefore, we conclude that the motor system is engaged automatically in the presence of graspable objects, even when these objects do not reach full conscious identification.

A second, quite surprising, finding of Experiment 2 is that there was no enhancement in motor excitability for graspable objects in the Long SOA condition. At this long interval, we would not expect the target to be affected by the AB. Indeed, accuracy was very high, confirming that the objects themselves were as effectively identified as in Experiment 1, where they were presented in isolation. In conjunction with the results of Experiment 1, the lack of MEP modulation by graspable objects in this condition, therefore, is most likely attributable to the presence of T1. A possible explanation for the lack of MEP enhancement is that it is caused by T1 being a nongraspable object. That is, identifying T1 may have led to a disengagement of the dorsal stream and downstream motor

Figure 4. Normalized MEP amplitudes in Experiment 2 (top) and Experiment 3 (bottom), expressed as a percentage of each participant’s grand mean. In all panels, the darker colors correspond to the graspable T2 conditions and the lighter colors correspond to the nongraspable T2 conditions. Solid bars indicate conditions with nongraspable T1 objects, and striped bars indicate conditions with graspable T1 objects. A and C show MEP amplitudes for T2 objects presented at the short and long SOA, and error bars indicate within-subject \( SEM \) difference between graspable and nongraspable objects at each SOA (Franz & Loftus, 2012). In both experiments, there was a significant interaction between T2 object type and SOA that was not modulated by T1 object type in Experiment 3. B and D show MEP amplitudes for correctly identified and missed T2 objects presented at the short SOA, and error bars indicate within-subject standard error for the overall difference between graspable and nongraspable T2 objects (Franz & Loftus, 2012). In both experiments, there was only a significant main effect of T2 type (graspable > nongraspable) that did not interact with target detection or with T1 type in Experiment 3.
areas, because this object is not associated with a grasp action. This disengagement may take several hundred milliseconds to build up and thus only become apparent at longer SOAs. This possibility was tested in Experiment 3, by adapting Experiment 2 to have both graspable and nongraspable T1 stimuli. If there is an inhibition because of disengagement of the motor system triggered by a nongraspable T1, this should disappear in conditions where T1 is a graspable object.

**Experiment 3**

**Behavioral Accuracy**

T1 and conditioned T2 accuracy data were analyzed separately using ANOVAs with SOA (Short vs. Long), T1 type (Graspable vs. Nongraspable), and T2 type (Graspable vs. Nongraspable) as within-subject factors.

As in Experiment 2, overall T1 accuracy was high (92.9%, \(SEM = 1.1%\)). There were no significant effects of T1 or T2 type (Fs < 1) or of SOA (\(F(1, 21) = 2.5, p = .131, \eta_p^2 = .11\)) and no interactions (Fs < 1).

The T2 data revealed a robust AB effect, with accuracy at the Short SOA (50.4%, \(SEM = 4.8%\)) significantly lower than at the Long SOA (82.1%, \(SEM = 2.1%\); \(F(1, 21) = 46.3, p < .001, \eta_p^2 = .69\)). There was an interaction between SOA and T2 type (\(F(1, 21) = 5.3, p = .031, \eta_p^2 = .20\)). This was due to T2 accuracy for nongraspable objects at the Long SOA (83%) being marginally higher than that of graspable objects (81.3%), although this comparison was not significant (\(p = .090\)). Importantly, there was no significant effect of T1 type on accuracy (\(F(1, 21) = 1.9, p = .187, \eta_p^2 = .08\)).

**MEP Amplitude**

Although in this experiment we collected baseline MEPs from trials that did not contain a T2, we present the data normalized to each individual’s grand mean, for consistency with Experiment 2. Analysis of the baseline data revealed no difference in MEPs recorded for T2 objects that followed graspable versus nongraspable T1 objects at either the Short or Long SOA. In addition, statistical analysis of the T2 MEP data normalized using the baseline trials yielded identical findings.

The normalized peak-to-peak MEP values were subjected to an ANOVA using the same factors as in the behavioral analysis: SOA (Short vs. Long), T1 type (Graspable vs. Nongraspable), and T2 type (Graspable vs. Nongraspable). Only trials in which T1 had been correctly identified were included. These data are presented in Figure 4C.

Overall, peak-to-peak amplitudes for graspable objects (101.5%, \(SEM = 0.7%\)) were significantly larger than for nongraspable objects (98.3%, \(SEM = 0.6%\); \(F(1, 21) = 6.0, p = .024, \eta_p^2 = .22\); see Figure 4C). In addition, we replicated our original finding of an interaction between T2 type and SOA (\(F(1, 21) = 5.1, p = .034, \eta_p^2 = .20\)). MEPs were again significantly larger for graspable (105.3%, \(SEM = 1.8%\)) than nongraspable (98.2%, \(SEM = 2.0%\)) objects at the Short SOA (\(p = .005\), but no such difference was observed at the Long SOA (Graspable: 97.6%, \(SEM = 2.1%\); Nongraspable: 98.4%, \(SEM = 1.6%\); \(p = .718\)). Crucially, there was no main effect of T1 type and no interactions involving this factor (Fs < 1).

A second ANOVA compared correctly identified and “missed” targets at the short SOA, using Target Detection (Correct vs. Missed), T1 Type (Graspable vs. Nongraspable), and T2 Type (Graspable vs. Nongraspable) as within-subject factors. Four participants were excluded from this analysis because of having too few trials (<3) in one of the conditions. No effects or interactions involving T1 type were found (ps ≥ .375). As expected, there was a significant main effect of T2 type, with larger MEPs for graspable objects (105.2%, \(SEM = 2.3%\)) than nongraspable objects (96.8%, \(SEM = 2.3%\); \(F(1, 17) = 12.5, p = .003, \eta_p^2 = .42\)). Neither the effect of Target Detection (\(F(1, 17) < 1\)) nor the interaction between Target Detection and T2 type (\(F(1, 17) = 2.3, p = .151, \eta_p^2 = .12\)) were significant. This replicates the findings of Experiment 2. As in Experiment 2, MEP amplitudes did not differ overall between graspable T2 objects that were correctly identified (103.8%, \(SEM = 3.5%\)) or missed (106.6%, \(SEM = 2.7%\); \(p = .295\)).

To sum up, Experiment 3 replicated the main findings of Experiment 2, while additionally demonstrating that having a graspable object as the T1 target did not have any influence on the results. We also replicated our original finding that the MEP enhancement is not present at the long SOA. This allows us to conclude that this finding is not due to the nongraspable nature of the T1 stimulus leading to some form of motor disengagement.

**Combined Analysis of Experiment 2 and Experiment 3**

Finally, given the lack of influence of T1 type on any of the effects reported, we also ran an analysis that combined the data from Experiment 2 with the data from the equivalent conditions of Experiment 3 (i.e., those with a nongraspable T1: \(NG^{T1}G^{T2}-\text{Short}\), \(NG^{T1}NG^{T2}-\text{Short}\), \(NG^{T1}G^{T2}-\text{Long}\), and \(NG^{T1}NG^{T2}-\text{Long}\)). This gave us more power to detect any effects that might have been missed in the individual experiments.

The accuracy analysis confirmed the presence of an AB, with accuracy at the Short SOA (54.9%, \(SEM = 3.6%\)) much lower than the Long SOA (84%, \(SEM = 1.5%\); \(F(1, 43) = 82.7, p < .001, \eta_p^2 = .66\)), as well as a mild deficit in T1 accuracy at the Short SOA (93.8%, \(SEM = 0.9%\)) compared with the Long SOA (95%, \(SEM = 0.7%\); \(F(1, 43) = 5.1, p = .029, \eta_p^2 = .11\)). No other T1 or T2 effects were significant (Fs < 1).

Analysis of the MEP data confirmed the significant main effects of SOA (\(F(1, 43) = 4.78, p = .034, \eta_p^2 = .10\)) and T2 type (\(F(1, 43) = 6.13, p = .017, \eta_p^2 = .13\)).
as well as a robust interaction between the two factors ($F(1, 45) = 9.21, p = .004, \eta^2_p = .18$). Breaking down this interaction revealed that, across the two experiments combined, MEP amplitudes were significantly higher for graspable (112.2%, $SEM = 2.8\%$) than nongraspable objects (97.2%, $SEM = 3.1\%$) at the Short SOA ($p < .001$). No such difference was observed at the Long SOA (Graspable: 93.1%, $SEM = 2.7\%$; Nongraspable: 96.8%, $SEM = 3.2\%$; $p = .345$). In addition, MEP amplitudes were higher for graspable objects at the Short SOA than those presented at the Long SOA ($p < .001$), whereas they did not differ for nongraspable objects ($p = .943$).

Comparing correct versus missed T2 MEP data at the Short SOA yielded an effect of T2 type ($F(1, 38) = 7.58, p = .009, \eta^2_p = .17$), with higher MEP amplitudes overall for graspable (111.9%, $SEM = 3.8\%$) compared with nongraspable objects (99.2%, $SEM = 3.6\%$). This effect was not influenced by whether the target had been correctly identified or not ($F(1, 38) < 1$).

Thus, combining the two experiments, we have robust evidence of enhanced MEPs in response to graspable T2 objects, irrespective of whether these objects are correctly identified or missed due to the AB.

GENERAL DISCUSSION

The main novel finding of this study is that the increased motor excitability in the presence of graspable objects that has been found in previous studies (e.g., Cardellicchio et al., 2011; Makris et al., 2011; Buccino et al., 2009) is also observed when these objects are not consciously identified.

The results of Experiment 1 replicate previous demonstrations that MEPS elicited while participants passively viewed images of graspable objects were significantly larger than those elicited by nongraspable objects (Cardellicchio et al., 2011; Makris et al., 2011; Buccino et al., 2009). Furthermore, this enhancement in motor excitability was equivalent for images presented very briefly (83 msec) and backward masked and for images displayed for a relatively long duration (500 msec). Note that in this experiment objects were identified with high accuracy regardless of exposure duration. Experiments 2 and 3 then investigated whether this enhancement is also observed when attentional control over object encoding is disrupted by the AB. The behavioral results confirmed that identification accuracy was substantially impaired for both graspable and nongraspable objects when they followed another target presented approximately 170 msec prior, consistent with an AB. The magnitude of this AB was comparable to that seen in many other studies that employed object stimuli (McNair & Harris, 2014; Harris et al., 2010; Dux & Harris, 2007). Despite this sizeable AB, MEPS elicited by graspable objects at the short SOA showed a similar enhancement relative to nongraspable objects as was found in Experiment 1, where the target object had not been subject to an AB.

This significant MEP enhancement for graspable objects was obtained both when the objects were identified correctly and when they were missed, and across the two experiments, we found no evidence that this enhancement differed in size between identified and undetected objects. Furthermore, MEPS in response to successfully identified objects were of similar magnitude to those elicited by missed targets. Finally, Experiment 3 demonstrated that neither the behavioral accuracy nor the size of the MEPS was influenced by action affordances of the T1 target object that preceded our object of interest. Taken together, these results indicate that the motor system is automatically engaged in response to graspable objects, even under conditions in which object detection and, thus, deliberate motor imagery or grasp preparation is unlikely (cf. Yu et al., 2014).

One potential caveat to this conclusion is that the graspable objects in our experiments were always depicted with the handle pointing toward the right. This was done to provide stimuli that were most conducive to grasping with the right hand and thus would readily engage the motor system in our right-handed participants. However, a consequence of this is that the most salient part of the graspable object—the handle—could have provided a consistent spatial cue biasing attention toward the right side of space and the right hand, possibly enhancing MEPS amplitudes. We believe this explanation is unlikely for a couple of reasons. First, previous studies of response compatibility effects with handled objects have established that these effects are not the result of a Simon effect (i.e., faster responding with the hand corresponding to the side of stimulus presentation; Masson, Bub, & Breuer, 2011; Symes, Ellis, & Tucker, 2005). Second, even though graspable objects such as tools can act as a spatial cue, this cueing effect is usually quite slow, taking about 400 msec to emerge (Roberts & Humphreys, 2011), and may in fact arise as a consequence of motor-related processing (Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003). This is too slow to influence the MEPS measured 250 msec post-target onset. In addition, disrupting attentional allocation to graspable objects did not influence the excitability of the motor system; we found no difference in MEP amplitudes between detected and undetected target stimuli presented during the AB. Given this, we would argue that the effects seen here are more likely to be specifically due to the motor affordances of the objects, although we cannot completely exclude other attributes that correlate with “graspability,” such as object shape and size.

Our findings are compatible with those of a previous study that measured motor priming effects in an AB paradigm (Pappas & Mack, 2008). In that experiment, graspable target items presented during the AB, whose handles were oriented toward either the left or right, facilitated faster finger press responses to a subsequent color or probe with the compatible hand. Consistent with the results of our experiment, this occurred even when the
target items were undetected by the participant. The present findings complement those of Pappas and Mack’s study by showing priming of the motor pathway when the task does not require preparation of a motor response and additionally provide direct evidence of the timing of the motor system engagement by graspable objects in a way that RT studies of motor priming cannot.

Our experiments demonstrate differential underlying cortical excitability for graspable versus nongraspable objects approximately 250 msec after the onset of the critical target, when the TMS pulse was applied to the primary motor cortex. The timing of the motor cortex involvement demonstrated here corresponds well with that found in other studies. For example, in an ERP study investigating mental transformations of tools and other objects, Petit et al. (2006) found evidence of neural activity 184–288 msec after stimulus onset that was source-localized to the motor cortex and was specific to the tool stimuli. Similarly, an ERP study by Proverbio, Adorni, & D’Aniello (2011) found differential neural activity in the post-central sulcus (somatosensory cortex) and premotor regions for tools compared with nonmanipulable objects 210–270 msec after stimulus onset. Although this timing may be considered by some to be quite late for “automatic” recruitment of the motor cortex by viewed objects via a rapid dorsal stream route, it is consistent with the idea that activation of grasp-related areas by tools and other graspable objects occurs after the objects have accessed identity representations in the ventral stream, which inform the types of functional grasps associated with those objects (Fabbri et al., 2016; Almeida, Fintzi, & Mahon, 2013).

Evidence for such an “indirect” route from vision to action was obtained in an fMRI study which showed activation in the inferior parietal lobe—which is linked with grasping and manipulation actions associated with objects (Vingerhoets, 2014)—in response to stimuli that were chromatically biased to be processed by the parvocellular system that projects almost exclusively to the ventral visual stream (Almeida et al., 2013). Functional connectivity analysis confirmed that activity in this region was principally associated with processing in the ventral processing pathway. It is worth stressing that in our study interrogating the motor cortex with TMS at 250 msec poststimulus allows sufficient time for the stimulus to be processed in perceptual areas of the ventral stream—which we know occurs for both detected and undetected items during the AB (Sergent et al., 2005; Marois et al., 2004)—while coinciding with the critical time point when items are undergoing consolidation in visual short-term memory. Previous studies have confirmed that stimuli that are missed during the AB show an attenuated, or absent, N2 and P300 components of the ERP; these components occur 200–500 msec poststimulus presentation and are associated with attentional selection and working memory encoding (Sergent et al., 2005; McArthur, Budd, & Mitchie, 1999). Therefore, our results provide critical evidence that at a time when a stimulus is most disrupted by the AB, with resulting significant impairments in conscious awareness of the stimulus, the motor cortex nonetheless demonstrates differential excitability in response to graspable versus non-graspable objects. We argue that this MEP enhancement for graspable objects is driven by perceptual representations in the ventral stream that were activated in equal measure for both identified and missed stimuli, even when these stimuli failed to reach conscious awareness.

A surprising finding of this study, observed in both Experiments 2 and 3, is that there was no enhancement in MEPs for graspable objects in the long SOA condition. Given that T2 was identified with high accuracy at this SOA and that comparably well-identified objects in Experiment 1 were associated with robust enhancement in motor excitability, this lack of MEP modulation can only be attributed to the presence of T1. Experiment 3 demonstrated that this lack of differential cortical excitability at the long SOA is not due to interactions between the motor affordances (or lack thereof) of T1 and T2, because the type of T1 object (graspable vs. nongraspable) did not modulate the MEP.

A plausible explanation is that the suppression of MEPs at the long SOA may be due to interhemispheric inhibition (IHI) resulting from preparing to make a mouse-click response with the left hand at the end of the trial. This preparation is triggered by the presentation of the T1 stimulus. Studies that examined IHI during muscle engagement have found that contractions of one hand can increase IHI from the contralateral to the ipsilateral hemisphere, resulting in smaller MEPs recorded from the opposite hand (Hinder, Schmidt, Garry, & Summers, 2010; Duque et al., 2007). Importantly, inhibition from movement preparation tends to occur toward the later stages of preparation, typically showing a relatively gradual ramping-up of inhibition across a period of 500–900 msec (e.g., Lebon et al., 2015; Duque, Labruna, Verset, Olivier, & Ivry, 2012; Duque, Lew, Mazzucchelli, Olivier, & Ivry, 2010; Giovannelli et al., 2009). This accounts for the fact that when graspable T2 targets are presented in temporal proximity to T1, they are less susceptible to inhibitory mechanisms and are associated with enhanced MEPs, whereas when T2 and T1 are timed to occur farther apart, the MEPs are suppressed to a level on par with nongraspable objects. Although this finding provides some intriguing evidence of the complex motor response dynamics invoked by multiple targets, it is incidental to our main question of interest, which is whether an objects’ action affordances automatically engage the motor system.

In conclusion, we found an enhancement in motor excitability when graspable objects were presented during a period of disrupted attention and encoding processes and irrespective of whether these objects were correctly identified or not. These findings provide direct neurophysiological evidence for the automatic recruitment of the motor system when passively viewing images of graspable objects for the purpose of identification.
APPENDIX 1

Experiment 1 Stimuli

Graspable objects: comb, cup, fork, frying pan, hammer, jug, paint brush, paint roller, pliers, scissors, screwdriver, spoon, teapot, toothbrush, watering can, wrench.

Nongraspable objects: book, bookcase, boot, chair, chessboard, clock, desktop, fan, hat, helmet, lamp, plant, rug, skateboard, speaker.

Experiment 2 Stimuli

Graspable T2: comb, cup, fork, frying pan, hammer, jug, paint brush, paint roller, pen, pliers, razor, salt shaker, scissors, screwdriver, spoon, spray bottle, teapot, toothbrush, watering can, wrench.

Nongraspable T2: bin, book, bookcase, boot, chair, chessboard, clock, desk, drawers, fan, hat, helmet, lamp, mailbox, plant, rug, skateboard, speaker, TV, watch.

T1 objects (nongraspable): barrel, bee, bench, bicycle, bird, butterfly, car, cat, clover, dog, duck, elephant, fire hydrant, fish, frog, hat, horse, hourglass, laptop, leaf, light bulb, luggage, motorcycle, printer, rabbit, rollerblade, shell, shirt, soccer ball, sofa, table, telephone booth, toilet, tractor, traffic cone, traffic light, vase, washing machine, wheel, zebra.

Experiment 3 Stimuli

Graspable objects (T1 and T2): comb, cup, fork, frying pan, hammer, jug, paint brush, paint roller, pliers, scissors, screwdriver, spoon, teapot, watering can, wrench.

Nongraspable objects (T1 and T2): book, bookcase, boot, chair, chessboard, clock, desk, drawers, fan, hat, helmet, lamp, mailbox, rug, skateboard, speaker.

Acknowledgments

This research was supported by Discovery Project grants DP120102299 and DP160102871 from the Australian Research Council as well as a Future Fellowship (FT0992123) awarded to I. M. Harris.

Reprint requests should be sent to Dr. Irina M. Harris, School of Psychology, Brennan-MacCallum Building A18, University of Sydney NSW 2006, Australia, or via e-mail: irina.harris@sydney.edu.au.

Note

1. Here and in subsequent experiments, we used ANOVA to analyze the accuracy data. Although it could be argued that a generalized linear mixed-model analysis might be more appropriate given the nature of the data, we opted to use ANOVA because it has greater currency in this literature and the identification accuracy was not the main focus of this study. Accuracy results were used to verify that participants were able to identify the objects under brief exposure in Experiment 1 and experienced an AB (i.e., accuracy at short SOA lower than that at long SOA) in Experiments 2 and 3. For this purpose, an ANOVA yields accurate information.

REFERENCES


