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Binocular vision enhances a rapidly evolving affordance priming effect: behavioural and TMS evidence.

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Abstract

Extensive research has suggested that simply viewing an object can automatically prime compatible actions for object manipulation, known as affordances. Here we explored the generation of covert motor plans afforded by real objects with precision (‘pinchable’) or whole-hand/power (‘graspable’) grip significance under different types of vision. In Experiment 1, participants viewed real object primes either monocularly or binocularly and responded to orthogonal auditory stimuli by making precision or power grips. Pinchable primes facilitated congruent precision grip responses relative to incongruent power grips, and *vice versa* for graspable primes, but only in the binocular vision condition. To examine the temporal evolution of the binocular affordance effect, participants in Experiment 2 always viewed the objects binocularly but made no responses, instead receiving a transcranial magnetic stimulation pulse over their primary motor cortex at three different times (150, 300, 450 ms) after prime onset. Motor evoked potentials (MEPs) recorded from a pinching muscle were selectively increased when subjects were primed with a pinchable object, whereas MEPs from a muscle associated with power grips were increased when viewing graspable stimuli. This interaction was obtained both 300 and 450 ms (but not 150 ms) after the visual onset of the prime, characterising for the first time the rapid development of binocular grip-specific affordances predicted by functional accounts of the affordance effect.

Keywords: Affordances, binocular vision, action priming, TMS, MEPs

1. Introduction

Determining the neural mechanisms that facilitate human interactions with manipulable objects is an important topic in psychology and neuroscience. Gibson's (1979) ecological theory of object perception and affordances is one of the most well-known approaches. According to this idea, all common manipulable objects, including tools, have properties that are automatically associated with specific actions. On this basis, simply viewing an object triggers congruent motor plans for interacting with it, even when there is no explicit intention to act. Automatic priming effects of this kind have since been described in a variety of selection-for-action paradigms, typically involving reaching and/or grasping movements (Castiello, 1999; Craighero et al., 1996, 1998, 2002; Creem & Proffitt, 2001; de'Sperati & Stucchi, 1997; Gentilucci, 2002; Tucker & Ellis, 1998). For example, Ellis and Tucker (2000) used as primes different real objects with action significance for either precision (pincer) or whole-hand (power) grasping. After viewing the primes for 700 ms, participants were asked to respond to imperative auditory stimuli signalling a precision or power grip action that was either congruent or incongruent with the prime. The results showed a significant interaction between object and response types; 'pinchable' and whole-hand 'graspable' objects selectively primed compatible precision and power-grip responses, respectively, even though the prime features carried no task-relevant information.

Employing a similar paradigm, we recently investigated the dynamics by which affordances evolve in the motor system when human subjects view pictures of objects with 'pinching', 'grasping' or 'no-action' (e.g., a bed) significance as primes (Makris et al., 2011). In the first experiment participants responded to orthogonal (i.e. non action-related) visual stimuli (changes of background colour of the picture) that cued a precision or power grip action, and with different stimulus onset asynchronies (SOAs) of 400, 800 or 1200 ms between the prime and imperative stimuli. The results showed that prime objects with action significance facilitated congruent responses, similar to Ellis and Tucker (2000), but only for the shortest SOA of 400ms. In a second experiment these findings were validated by applying a standard methodology measuring corticospinal excitability. This time, the same prime objects were presented while stimulating the participants' primary motor (M1) cortex via single-pulse transcranial magnetic stimulation (TMS) at an SOA of 300, 600 or 900 ms, while motor evoked potentials (MEPs) were recorded from specific muscles of their opposite hand. This methodology exploits the fact that peak-to-peak MEP (i.e., muscle twitch) amplitudes increase during increasing M1 preparation for the related movement, and so provide an index of covert motor planning (e.g., Hadar, Makris & Yarrow, 2012; Izumi et al., 1995). Participants viewed the objects passively and MEPs generated by the

TMS pulse were recorded from two muscles selectively associated with pinching and power grips. Muscle twitches were larger when participants viewed the objects affording actions involving that particular muscle, but only for the shortest (300 ms) SOA between the prime and TMS pulse.

These data together suggest that affordances for action develop quickly in M1 cortex, within a 300-400 ms period following prime onset, and are also actively suppressed or passively dissipate quite rapidly, since we were unable to demonstrate them at SOAs of 600-800 ms. Such a rapid evolution and decay makes functional sense, because a more persistent intention to act that is never implemented might well interfere with the motor system's ability to form new motor plans when subjects direct their visual attention to a different object. However, while this is consistent with related neurophysiological studies showing that affordances can emerge only 200-250 ms after priming (Buccino et al., 2009; Proverbio et al., 2011), it is unclear why our pictorial object presentations appeared to generate concordant affordance effects which were absent at SOAs corresponding to the time at which Ellis and Tucker's (2000) experiments, employing real-world objects as primes, were able to demonstrate them.

One possibility is that real objects presenting three-dimensional (3D) structural information about their properties generate different – and perhaps, more robust and veridical – affordance effects than do two-dimensional (2D) pictorial representations of the same objects. In fact, there is rather limited research on how different types of vision affect object affordances, with most of the existing literature using 2D pictures as primes. However, evidence obtained by Castiello et al. (1998), in which subjects were required to reach out and grasp a 3D or 2D representation of the same object (an apple) supports this possibility. Their key findings were that participants spontaneously planned and executed a whole-hand (power) grip when grasping the object perceived as having 3D (depth) structure – just as they did when grasping a real apple – but adopted a *precision* grip when grasping the simpler 2D image of the same apple, as if it were just a disc, without specific connotations for what the depicted object afforded (Castiello et al., 1998). Cardellicchio et al. (2011) have also recently presented evidence that the 3D structure of the scene in which objects are presented influences the intention to act. They recorded MEPs induced by M1 cortex TMS stimulation in participants viewing graspable or non-graspable objects located at distances that were within or outside the subject's reachable 3D space, and obtained concordant affordance effects (i.e., bigger MEPs) only for graspable objects in near-reaching space.

In contrast to the 'priming' literature, the different types of vision employed for planning and guiding *overtly executed* reaching and grasping actions has received considerable attention over the past two decades. In their seminal study, Servos et al. (1992) tested the differences between binocular and monocular vision for performing these object-directed actions. They found that movement preparation (reaction) and execution times under monocular viewing (with the other eye occluded) were both more protracted and less accurate compared to those performed under binocular conditions. Similar studies by others have replicated these principal findings (e.g., Watt & Bradshaw, 2000; Loftus et al., 2004; Melmoth & Grant, 2006), and have established that the additional depth information provided by retinal disparity when viewing binocularly, and known to improve perceptual estimates of 3D scene and object geometry, is also key to the efficiency of planning and guiding natural (i.e., ecologically-relevant) goal-directed grasping actions (Castiello & Begliomini, 2008; Melmoth et al., 2007, 2009; Sakata et al., 1997). Indeed, Knill (2005) has shown that subjects generally attach more weight to binocular than to pictorial (monocular) depth information for these purposes than they do for perception, even when the two sets of cues are placed in conflict (but see Keefe et al., 2011).

Because affordances are generated quickly and automatically, without complex mental effort, it is likely that they are mediated by direct ‘dorsal stream’ pathways projecting from primary occipital visual to posterior parietal areas and on to frontal motor cortices, while bypassing ‘ventral stream’ areas more associated with conscious object identification processes (Milner & Goodale, 1995). Castiello et al. (1998) made this very case, arguing that their participants would have used their whole hand to grasp the 2D apple had they accessed a semantic representation of it when planning their grip, and the case is further supported by neuroimaging studies showing positive correlations between affordance effects and neural activity in parieto-frontal brain areas (Grezes et al., 2003; Valyear et al., 2007). Consistent with Knill (2005), there is also evidence of a functional dorsal stream primacy for processing binocular depth cues for grasping actions. More specifically, functional imaging studies indicate that posterior parietal areas normally mediate this behaviour (Binkofski et al., 1999; Chao & Martin, 2000; Grafton et al., 1997; Cavina-Pratesi et al., 2007) without recruiting perceptual representations, *except* when using monocular vision (Verhagen et al., 2008); under these conditions, and with increasing demand to employ 2D pictorial cues for the purpose, ventral stream activations are increased and appear to be functionally integrated into the grasping plan. This binocular specialization may also explain why the famous visual agnosic subject, DF, who suffered extensive ventral stream damage some years ago, has no difficulty grasping objects under natural binocular conditions via her intact dorsal stream system, but is severely impaired when her vision is restricted to one eye (Marotta et al., 1997).

1.1. Rationale for the current experiments

With these considerations in mind here, we adapted our previous methods (Makris et al., 2011) to conform more to those of Tucker and Ellis (2000), by using real ‘pinchable’ or ‘graspable’ objects as primes and auditory stimuli as congruent or incongruent imperative cues. In Experiment 1, participants viewed the presented objects monocularly or binocularly at a fixed SOA of 500 ms; that is, at an intermediate time for the affordance effects observed in these two previous studies. In Experiment 2, subjects passively observed the objects binocularly while receiving single-pulse TMS over M1 cortex at different times (between 150-450 ms) relative to prime onset. As before, we simultaneously recorded MEP amplitudes from two muscles of their opposite hand – one (*first dorsal interosseus*; FDI) involved in pinch grips and the other (*abductor digitorum minimi*; ADM) associated with power grasps – in order to expand upon previous findings regarding the temporal dynamics of covert motor planning under more ecologically-appropriate conditions.

2. Experiment 1

2.1. Methods

2.1.1. Participants. Eighteen healthy subjects (14 females; Mean age = 20.9, SD = 4.2) participated in the experiment in exchange for either course credit or cash payment. Seventeen were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) (Mean Lateralisation index (LI) = 0.92, SD = 0.09) and one participant was left-handed (LI = -0.59). The dominant eye in each subject was determined by a conventional sighting-eye test procedure. We asked the subjects to hold their arms in front of them and to form a triangle by overlapping the space between index finger and thumb with the same space on their opposite hand; then we asked them to look at a door knob through the triangle hole formed by their hands and focus just on the object; finally, we instructed them to close one of their eyes and report whether they could still the object; if they could still see it with their left-eye open they were classified as left-eyed and vice versa for the right eye. All subjects were naïve as to the purpose of the experiment. The experimental procedures were approved by the City University London Psychology Department Ethical Committee, and all participants gave their informed consent before beginning the study.

2.1.2. Material/apparatus. The prime set consisted of twelve real objects; six objects associated with a precision grip and six objects associated with a power grip (see Appendix A for a list of objects). Prime stimuli were placed on the top of a large yellow sponge one at a time by the experimenter, who followed a presentation sequence that was randomised for each participant. The response device was adapted from the Ellis and Tucker (2000) and Makris et al. (2011) studies. It consisted of a plastic cylinder, at the top of which a small pressure-button was attached, so that each time the cylinder was squeezed with a power grip the button would be pressed. The second component was a small plastic pressure-switch that was taped to the inside tip of the participant's thumb. Participants were instructed to hold the device with their dominant hand, holding the switch with their index finger and thumb, and grasping the cylinder with the remaining three fingers against their palm. This way, responses with the cylinder or the small switch would mimic power or precision grips respectively. Finally, participants wore a pair of Plato liquid crystal shutter goggles (Translucent Technologies; Toronto, Ontario, Canada) so that vision could be controlled by opening one or both lenses at specific times.

<INSERT FIGURE 1 AROUND HERE>

2.1.3. Design and procedure. The experiment was implemented and controlled by a PC running E-Prime Software version 1.1 (Psychology Software Tools, Inc., Pittsburgh, PA, 2002), which also controlled the opening and closing of the shutter goggles and recorded response times. After having their handedness assessed, participants were seated comfortably in front of a desk, at a distance of approximately 50 cm in front of the object presentation point (maintained with a chin rest). Following a brief demonstration of how to hold and use the response device, they had a short practice session (of approximately 20 trials). Once they displayed a good understanding of the experimental task and how to use the device, the actual experiment started. As schematised in Figure1, each trial started with the goggles shut while the experimenter (who sat off to one side) placed a prime object on the presentation point. With the object in place, either one (always the dominant eye) or two lenses would open. The stimulus-onset asynchrony (SOA) between the glasses opening (to reveal the prime) and the onset of the imperative stimulus (the *target*) was set at 500 ms. The target was a high or low-pitched pure tone (duration 1 sec; high-pitch frequency 1000 Hz; low-pitch frequency 200 Hz). Participants were instructed to press the cylinder for a high-pitched sound and the small switch for a low-pitch one (with the opposite mapping used for half of the sample). The goggles remained open and the prime object visible until the participant gave a response, at which point the glasses closed again, giving the experimenter enough time (approximately ten seconds) to place a new object.

In order to maintain participants' attention on the presentation point and prime objects, we introduced a vigilance task. On some trials, the goggles would open, but no object had been placed on the sponge. In that case participants were instructed to withhold their responses to the subsequent tone. Overall there were 162 trials; 144 experimental trials (3 repeats of each object x 6 primes per object category x 2 prime object categories [precision/power] x 2 viewing conditions [monocular/binocular] x 2 targets [low/high pitch]) and 18 vigilance trials (half monocular and half binocular, with the target tone selected at random), divided into 3 blocks. Each participant received a different random ordering of the 162 trials. After the end of the experiment all subjects were debriefed and compensated for taking part in the study.

2.2. Results

<INSERT FIGURE 2 AROUND HERE>

For the purposes of our analysis, low/high pitch targets were re-coded based on the type of response they directed (i.e. a precision or power grip). Median reaction times (RTs) were then calculated using the correct responses for each participant in each condition, and are shown in Figure 2. These data were examined with a 2 (viewing condition) x 2 (prime object) x 2 (response type) repeated-measures ANOVA. There were no main effects or significant 2-way interactions, but there was a significant interaction between the three factors [F (1, 17) = 9.56; p = 0.007; η^2 = 0.36]. To explore this further, we ran separate 2 (prime object) x 2 (response type) ANOVAs for each of the two viewing conditions. For binocular viewing, the results showed a significant interaction between prime object and response type [F (1, 17) = 8.45; p = 0.01; η^2 = 0.33]. Here, *post-hoc* t-tests revealed that precision-grip RTs were significantly faster (by ~20 ms) for congruent pinchable object primes (M = 554, SD = 68) compared to incongruent graspable ones (M = 576; SD = 66) [t (17) = 2.29; p = 0.035], and that power-grip responses were significantly faster (by ~35 ms) for graspable primes (M = 547, SD = 74) than for objects associated with a precision grip (M = 583, SD = 65) [t (17) = 2.23; p = 0.04]. In other words, binocular viewing elicited clear affordance effects for both prime categories, as reflected in the RTs for different types of grasp. However, affordance effects were not found in the monocular vision condition, for which the ANOVA revealed no comparable prime x response interactions. Indeed, if anything, there was a trend in the opposite direction for precision-grip responses (see Figure 2), for which congruent RTs were the longest of the four prime-response combinations.

<INSERT TABLE 1 AROUND HERE>

A complementary analysis applied to mean error rates derived from the proportion of incorrect responses (see Table 1) did not suggest that the RT results were driven by a speed-accuracy trade-off. There were no significant main effects or interactions in the three-way ANOVA, but the trend was broadly consistent with the RT data. For the binocular vision condition, error rates were higher for incongruent trials (i.e. power-grip responses to pinchable objects and precision-grip responses to graspable objects) than for congruent power-grip or precision-grip responses, whereas for monocular viewing, these same trends were absent (Table 1) but hinted at increased errors for *congruent* compared to incongruent precision-grip responses. More specifically, then, participants did not delay their monocular reaction to the congruent precision-grip combination (Figure 2) because they spent longer evaluating the prime before making the ‘correct’ choice. Further analyses also showed that incorrect responses did not occur significantly more or less often for a few of the primes that might be considered to have less familiar grasping associations (e.g., the tea-box; safety razor cover) than the other more common objects (e.g., the glass; battery).

2.3. Discussion

We sought behavioural evidence for the automatic generation of covert motor action plans when subjects viewed real 3D prime objects binocularly or monocularly during 500 ms SOA. Statistical analysis showed that binocular prime viewing automatically afforded appropriate grasping actions; participants were significantly quicker to produce precision-grip responses when primed by observing congruent ‘pinchable’ compared to incongruent ‘graspable’ objects and *vice versa* when making power-grip responses. These results *largely* concur with Ellis and Tucker (2000) who also had subjects view real 3D ‘pinchable’ or ‘graspable’ object primes binocularly, but with a longer SOA of 700 ms. Their results also revealed a two-way interaction, but one in which the difference in median choice RTs for congruent *versus* incongruent precision-grip responses was smaller (~4 ms) than for compatible *versus* incompatible power grips (~15 ms). Our results for these two object prime categories were in the same direction (Figure 2), but the absolute differences between the relevant median choice RTs were substantially greater (~20 ms and 35 ms, respectively). The increased size of our effects is of direct relevance to our rationale concerning the neural dynamics of affordances, as they are consistent with a decay in covert motor plans for action when objects – even when presented as 2D pictures (Makris et al., 2011) – are continuously viewed binocularly for longer than 400-500 ms.

There was, however, another important procedural difference between the two studies that may have influenced the affordance effects. This is that while we aimed at ensuring our subjects' attention to the prime objects by interleaving vigilance (i.e., no-prime catch) trials among the experimental presentations, Ellis and Tucker (2000) did this by requiring their participants to perform a *post hoc* test involving recalling objects from a set that had been either used as primes or not previously seen. This, by its nature, presumably introduced their subjects to a cognitive load in consciously identifying the objects presented during the experiment, with potential interference in the priming process, whereas our experiment did not.

Our major new finding is that monocular viewing of the same 3D primes elicited no demonstrable concordant affordances. We do not, of course, wish to imply by this that monocular vision results in an inability to generate covert motor plans, only that the key standard metric employed – a difference in median choice RTs for congruent *versus* incongruent responses – failed to show compatible priming effects. One possible reason for this is that congruent monocular affordances, equivalent to those generated by binocular vision, did initially emerge, but decayed so rapidly within the 500 ms SOA after prime onset that they no longer influenced our subjects' choice RTs to the imperative stimuli. However, there is evidence that the processing of monocular, pictorial, information for other automatic activities associated with grasping – namely, 'on-line' movement corrections necessary to respond quickly to sudden object perturbations – takes significantly *longer* than under binocular viewing (Greenwald et al., 2005), so a *delayed* onset in the development of monocular affordances would be more likely. Nonetheless, rapid monocular decay within the 500 ms SOA cannot be entirely discounted, given our previous evidence (Makris et al., 2011) that affordances elicited by binocular viewing of 2D pictures are present at 400 ms, but absent at 600 ms, after prime onset.

We believe that a more likely explanation relates to the 'uncertainty' engendered about the 3D structure – and, hence affordances of – the prime objects when they were viewed under the reduced/degraded cue conditions of monocular vision. The perceptual literature on binocular and monocular cue-integration for reliably estimating the 3D properties of objects has consistently shown that they are normally combined in a statistically optimal fashion (reviewed in Landy et al., 1995), so that removing the availability of either type of visual information impairs these judgements (e.g., Johnston, 1991; Hollis et al., 2004). Recent evidence shows that similar mechanisms of depth-cue combination normally operate in visuomotor systems, since the efficiency of both the planning and overt execution of grasping movements are compromised by reducing/degrading either the binocular or monocular information available for these purposes (Greenwald & Knill, 2009; Keefe et al., 2011; Knill, 2005; Melmoth et al., 2007; Servos & Goodale, 1992). In our experiment, both types of information were available for determining the 3D prime properties in the binocular condition, but only (or mainly) pictorial information when viewing with one eye, so that any affordance effects generated may have been too weak or subtle to demonstrate via our choice RT paradigm.

These considerations may also help explain why we were previously able to demonstrate an effect with binocular viewing of 2D images (Makris et al., 2011). Under these conditions, some binocular information would have been available to the subjects – for example, vergence cues to the fixation distance and disparities in the two eyes generated by more peripheral elements of the pictures (e.g., Greenwald & Knill, 2009) – along with more obvious monocular pictorial cues to the object's identity, perhaps placing them intermediate between the binocular *versus* purely monocular conditions of the present study. Consistent with this, the overall binocular affordance effects elicited by the 2D primes in Makris et al. (2011) were numerically smaller (mean choice RT differences ~11 ms at 400 ms SOA) than in the current study (~29 ms at 500 ms SOA). Numerous other minor differences in methodology between the two studies, however, mean that this conclusion must remain a cautious one.

Indeed, the pattern of results we obtained across the two studies (i.e. reduced effects elicited by binocular viewing of photographic images relative to real objects) might arise because of the immediacy with which the object under observation is revealed to be only 2-dimensional and, thus, of equivocal grasping affordance (e.g., Castiello et al., 1998).[1] According to this perspective, it may not be the enhanced *quality* of the binocular depth cues that accounts for the reduced affordance of picture primes, but the automaticity of the evidence provided that the subject is looking at a 2D image. Under this account, the distinction between 2D and 3D object interpretation

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[1] We thank an anonymous reviewer for suggesting this possibility.

may be less marked with monocular vision alone, so that a reverse enhancement of congruent affordance effects might be obtained with monocular compared to binocular viewing when pictures are used as primes. Further research employing a direct comparison of monocular and binocular vision of both images and real objects is needed in order to fully address the plausibility of this alternative account.

Either way, our current findings clearly show that affordances arise more robustly with binocular viewing of real 3D objects than with monocular vision. Since in this experiment participants were actively responding to visual stimuli, one might ask whether these findings would also hold in conditions where there is no requirement for a motor response. More critically, it is not yet clear how affordances initially develop over time in ecologically-valid (i.e., binocular) conditions for object viewing, particularly in the temporal window immediately after prime onset. For both of these reasons, we ran a second experiment, which involved subjects passively viewing the same 3D objects used in Experiment 1 with both eyes, while receiving TMS at one of three different intervals after prime onset.

3. Experiment 2

3.1. Methods

3.1.1. Participants. A different group of 18 subjects (13 females; Mean age = 24.9, SD = 5.6) participated in the second study. The TMS protocol was approved by the City University London Psychology Department Ethical Committee. Prior to taking part in the experiment, all participants completed a medical questionnaire, screening for neurological and other medical problems, as well as other contraindications to TMS. Informed consent was obtained from all participants found eligible for the study. They were also assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) and were all found to be right-handed (Mean Lateralization index (LI) = 0.97, SD = 0.07).

3.1.2. Material/apparatus. The prime stimulus set and goggles configuration were the same as in Experiment 1, except that both lenses were programmed to open on every trial.

3.1.3. Transcranial Magnetic Stimulation (TMS) and electromyography (EMG). Participants viewed real objects (Appendix A) while receiving magnetic stimulation over their left hemisphere hand motor area. Evoked muscular responses (MEPs) were recorded from two intrinsic hand muscles [first dorsal interosseous (FDI) and abductor digiti minimi (ADM)] using electromyography (EMG). TMS was delivered via a 70 mm figure-of-eight coil (external casing diameter ~90 mm for each loop) connected to a Magstim Rapid^2 biphasic stimulator (The Magstim Co. Ltd., Whitland, Carmarthenshire, U.K.). The coil was held tangentially to the skull, with the handle pointing backwards/laterally approximately midway between the saggital and coronal planes. EMG was recorded using a DataLINK 13-bit data acquisition unit sampling at 1000 Hz with a band-pass filter applied (20-450 Hz), connected via two SX230FW amplifiers to 22x28 mm silver/silver chloride disposable electrodes. EMG was recorded and analysed on a dedicated PC using DataLINK analysis software version 7.5 (Biometrics Ltd., Ladysmith, VA, U.S.A., 2008). The protocol was implemented and controlled by E-Prime version 1.1 software (Psychology Software Tools, Inc., Pittsburgh, PA, U.S.A., 2002) running on a second PC, which delivered digital TMS signals and controlled the opening of the goggles.

The location of the primary motor cortex “hot spot” for activating muscles of the hand was determined prior to the main experiment. This was achieved by trial and error exploration relative to its typical location, with single-pulse TMS applied at a low rate (<0.2 Hz). We first found a location that consistently gave rise to an MEP in FDI, and then determined the lowest stimulation intensity that gave rise to this activation during rest on at least 50% of occasions (the “resting motor threshold”). We then adjusted the position of the coil slightly in order to achieve consistent MEPs in both muscles, which typically required stimulation at around 110% of passive motor threshold (across subjects, stimulator output ranged from 50% to 85%; 110% - 120% of passive motor threshold).

<INSERT FIGURE 3 AROUND HERE>

3.1.4. Design & Procedure. As in Experiment 1, participants sat comfortably at a distance of 50 cm (maintained with a chin rest) in front of the object presentation point (a sponge), but with their dominant hand now in a relaxed position. As schematized in Figure 3, each trial started with the goggles shut while an experimenter placed an object on the presentation point. After this time, both lenses of the LCD goggles opened. TMS was delivered (with the coil held by a second experimenter) at three different SOAs of (150, 300 and 450 ms) relative to the visual onset of the prime. Immediately after that, the glasses closed again while the experimenter placed a new object at the presentation point. Note that we previously demonstrated compatible affordance effects between (2D) prime onset and TMS stimulation at an SOA of 300 ms, but not 600 ms or longer (Makris et al., 2011). The three intervals selected here were thus aimed to better examine the anticipated early temporal evolution of affordance priming, with the 450 ms SOA also very similar to the one (500 ms) interval employed in Experiment 1.

Also as in Experiment 1, in order to maintain the participant’s attention on the presentation point we introduced a vigilance task, during which the goggles opened, but no object was placed on the sponge. In this experiment no responses were required, so participants were instead instructed to keep track of the number of such occurrences throughout the experiment. TMS was delivered on these trials, but was not analysed. Overall there were 108 experimental trials (3 repeats of each object x 6 stimuli per object category x 2 prime object categories x 3 SOAs) and 18 vigilance trials (6 repeats of 3 SOAs). Participants were given a break every 30 trials. All experimental conditions, including the vigilance trials, were presented in a randomised order. After the end of the experiment all subjects were debriefed, and completed a short questionnaire stating any problems and/or discomfort caused due to TMS. Four participants reported mild discomfort as a result of induced muscular twitching on the scalp, but no major adverse events were reported or evident (these data are included in the larger summary of adverse events reported in Hadar, Makris & Yarrow, 2011).

3.1.5. Data analyses. All EMG recordings were first inspected for any significant muscular activity in the window from 300 ms prior to delivering the TMS pulse. Trials with any signs of EMG pre-activation that may have compromised the recordings were removed from the analysis. The data from five participants were discarded as the removed trials exceeded 10% of all trials. For the rest (N=13), peak-to-peak amplitudes of the MEPs obtained from each muscle were calculated on each trial and the median determined within each condition for each participant.

3.2. Results

<INSERT FIGURE 4 AROUND HERE>

In natural prehension, the FDI muscle is most closely associated with a precision grip, whereas the ADM muscle is more closely associated with a power grip. To examine their differential activations in our experiment, the median MEP amplitudes obtained were analysed with a 2 (FDI/ADM muscle) x 2 (prime object) x 3 (TMS SOA) repeated-measures ANOVA, with the Greenhouse-Geisser correction applied for violations of sphericity. This revealed a significant main effect of SOA [F (1, 12) = 4.72; p = 0.019; η^2 = 0.28] and a two-way interaction between muscle and prime type [F (1, 12) = 11.29; p = 0.006; η^2 = 0.49]. Importantly, the three-way interaction was also significant [F (1, 12) = 3.81; p = 0.036; η^2 = 0.24], indicating that there were differences between the extent of muscle activation by the different prime objects which also depended on the interval between prime onset and TMS pulse.

For this reason, we ran separate 2 (muscle) x 2 (prime) ANOVAs for each of the three SOAs. As shown in Figure 4, this analysis showed no muscle x prime-object interaction for the shortest SOA of 150 ms, and hence no differential priming effect of ‘pinchable’ and ‘graspable’ primes on evoked responses for the two muscles. By contrast, the ANOVAS for the stimulation times of 300 ms [F (1, 12) = 12.09; p = 0.005; η^2 = 0.5] and 450 ms [F (1, 12) = 13.46; p = 0.003; η^2 = 0.53] showed significant interactions between type of muscle and prime object, both of which were in the direction of concordant effects of priming upon the precision (FDI) and power (ADM) grip responses (Fig.4). For the 300 ms timing condition, *post-hoc* t-tests revealed that FDI MEPs were significantly bigger for objects associated with a precision grip (M = 0.35, SD = 0.13) than for “graspable” objects (M = 0.25, SD = 0.09) [t (12) = 3.17; p = 0.008], with the corresponding reverse trend, which did not quite achieve statistical significance, suggesting larger ADM MEPs for “graspable’” objects (M = 0.28, SD = 0.17) compared to “pinchable’” ones (M = 0.22, SD = 0.11) [t (12) = 1.52; p = 0.16]. However, for the later 450 ms timing condition, the *post-hoc* t-tests revealed both that FDI MEPs were significantly bigger for objects associated with a precision grip (M = 0.33, SD = 0.14) than for “graspable” objects (M = 0.25, SD = 0.14) [t (12) = 2.33; p = 0.038], and that ADM MEPs were significantly larger for object affording a power grip (M = 0.23, SD = 0.11) compared to ‘pinchable’ objects (M = 0.18, SD = 0.1) [t (12) = 2.99; p = 0.011]. Finally, a complementary ANOVA applied to trial removal rates (i.e. proportion of trials excluded due to signs of EMG pre-activation) across the different timing conditions showed no significant main effects or interactions.

3.3. Discussion

Our second experiment investigated the onset of affordances for real objects under natural binocular viewing conditions by using a TMS/MEP paradigm to track how motor plans developed in primary motor cortex when there was no requirement to make an action of any kind. The data showed a significant interaction between type of object and muscle: motor evoked potentials from the FDI muscle most associated with a precision grip were bigger when viewing ‘pinchable’ objects compared to ‘graspable’ ones, and *vice versa* for the ADM muscle most associated with a power grip. These affordance effects were not present at the shortest 150 ms SOA, but evident for stimulation times of 300 ms and 450 ms after prime onset, thus showing that the priming effect develops rapidly over time. These results broadly validate our reaction-time findings from the first experiment (i.e., a binocular affordance effect at 500 ms SOA). They are also consistent with previous measures of corticospinal excitability using TMS protocols with regards to affordances generated by binocular viewing of 2D primes. Such studies have presented tools with either complete or broken (i.e., ‘non-graspable’) handles (Buccino et al., 2009) and also objects similar to those used here, with either precision or power grip significance (Makris et al., 2011). In these studies, viewing pictures of the objects affording the appropriate action – for example, tools with intact handles oriented so as to facilitate the grasp – resulted in bigger MEPs from muscles associated with the compatible action at brief SOAs of 200 ms (the only interval examined by Buccino et al., 2009) and at 300 ms, but not 600 or 900 ms post-prime (Makris et al., 2011).

4. General discussion

Our data have clearly demonstrated that the sight of a real object can elicit motor plans for actions associated with it, even in cases where there is no intention to implement these actions. In order to assess this, we used as primes 3D objects that are associated with pinching or power grasping movements and applied two different paradigms, one based on choice reaction times and another measuring corticospinal excitability. Furthermore, we investigated, for the first time, affordance effects mediated by binocular (i.e., natural) compared to monocular vision, and at different times relative to binocular prime onset. Results from both experiments are in general accordance with Gibson’s (1979) theory of affordances and previous research supporting the existence of this phenomenon.

One consistent finding between our study and previous experiments is the rapidity with which the affordance effect develops. Neural mechanisms seem to generate a plan for action almost immediately after visual representation of manipulable objects. While it is possible to investigate the onset of affordances using purely behavioural studies, the unknown processing time associated with the imperative target stimulus blurs the resulting estimate of the true (neural) SOA. This is because, in the RT data of a behavioural task, we are in fact assessing the interaction between motor plans evoked by the prime and the target, which may themselves have different temporal profiles. If the motor pathway for the target is longer (quite possible, given the often arbitrary nature of the instructed task) it is feasible that an effect could even be obtained at a negative SOA. Hence direct neural measures as provided by TMS and event-related potential (ERP) approaches are to be preferred. Across the few studies that have addressed this issue, it is now possible to place an estimate on the latency of the affordance effect (including under binocular viewing conditions); it arises later than 150 ms, but is definitely present at 200-300 ms following the presentation of any (2D or 3D) object affording a grasping action (Buccino et al., 2011; Makris et al., 2011; Proverbio et al., 2011; present results). This latency for the onset of object affordances is consistent with the minimal time needed in order to generate activity in M1 for both intentional and automatic action plans. For example, electrophysiological studies investigating the development of the lateralised readiness potential, elicited whenever a subject prepares a movement with their hands (or feet), as well as TMS studies looking at how MEPs develop within the reaction time period, have indicated the onset of motor activity at approximately 200 ms following the initial presentation of a simple imperative stimulus with high stimulus-response compatibility, such as an arrow (Eimer & Schlaghecken, 1998; Verleger et al., 2009).

The subsequent decay time, during which the motor plan is actively suppressed or passively dissipates despite continuous viewing of the prime, is, however, less certain. Our evidence, along with the interpretations of Ellis and Tucker (2000), suggest that covert action plans are initially sustained for the period between 200-500 ms after prime onset, and then undergo an abrupt decline, so that they are undetectable or weak shortly afterwards (e.g., at 600-800 ms SOAs; Ellis and Tucker, 2000; Makris et al., 2011; present results). However, there is contrary evidence (Phillips & Ward, 2002; Symes, Ellis & Tucker 2007; Vingerhoets et al., 2009) suggesting that affordances are much more long-lasting. This evidence clearly bears further discussion.

Phillips and Ward (2002) obtained differences between choice reaction times when the hand of response was congruent *versus* incongruent relative to the left/right orientation of a prime object's handle. This congruency effect increased from an SOA of 0 to 400 ms and was at least maintained across SOAs of 400, 800 and 1200 ms between the onset of the prime and a lateralised imperative stimulus. Vingerhoets et al. (2009) tested the same SOAs (with the exception of 0 ms) and found persistent RT differences between graspable and non-graspable object primes against a background of gradually decreasing average RTs. However, in both of these studies we might question whether the effects are sufficiently specific to be able to properly define the time course of affordances. Phillips and Ward used clearly lateralised primes with left/right hand button presses and non-orthogonal targets, inviting explanations in terms of Simon-like spatial correspondences or spatial attentional cuing (cf. Anderson, Yamagishi & Karavia, 2002; Cho & Proctor, 2010; Riggio et al. 2008). Indeed they themselves favoured such an explanation, finding equivalent priming effects even when responses were made with the feet rather than the hands. Meanwhile Vingerhoets et al. (2009) failed to find any of the predicted *congruency* effects at all (perhaps because they had taken trouble to orient their response buttons vertically rather than horizontally), so their affordance effect may actually represent a general priming of RTs, rather than a specific interaction between objects and different classes of action.

However, Symes, Ellis and Tucker (2007) did obtain a hand x prime-orientation interaction that persisted at 800 and 1200 ms SOAs despite using rotated baton stimuli and additional control experiments designed to rule out Simon effects and the spatial cuing of attention. On the one hand, it would seem functionally maladaptive to generate long-lived covert action plans, most of which will not be executed, every time we observe an object with grasping affordance. On the other hand, it is intuitively appealing to consider that prolonged viewing of an object for a second at a time (or longer) would gradually facilitate an appreciation of its affordances that might then, from a functional perspective, enhance the conversion of the covert intention to act into a final decision to actually go-ahead and grasp it. Contrary to this appeal, data from Vingerhoets et al. (2009) suggests that affordance effects are not improved by the increasing the observer's functional or semantic knowledge about the prime, but depend upon more direct and automatic visual processing of the object's physical attributes. This is consistent both with our findings in Experiment 1 that the opportunity to combine binocular and monocular sources of depth information to more reliably establish the prime object's 3D properties during natural viewing with both eyes results in the generation of more robust affordances than the reduced depth-cue conditions of monocular vision, and with neuroimaging and other evidence that affordances do not evolve in ‘conceptual knowledge’ brain systems (e.g., Castiello et al., 1998; Valyear et al, 2007; Vingerhoets 2008). Hence we suggest that differences may exist between the persistence of the affordances revealed by lateralised key-press responses made to stimuli affording left or right-handed grips (as used by Symes, Ellis & Tucker 2007) and the highly specific “micro” affordances revealed in pinch/grasp paradigms based on Ellis & Tucker’s (2000) approach (and used here). This latter category of affordances appears to undergo quite rapid dissipation or suppression, which seems most consistent with a functional role tied to optimising real-world motor activity.

In conclusion, the present study investigated the temporal integration of visual and motor processes underlying object affordances, a phenomenon of continuing interest within the fields of psychology and neuroscience. We have provided further evidence regarding the time course of the affordance effect, particularly its initial rapid development under natural conditions involving the binocular viewing of real 3D objects, as well as demonstrating that these conditions evoke stronger affordances than with the more impoverished visual information available with just one eye. It has been estimated that 10% or more of the adult population have reduced or absent binocular vision (Richards, 1970) due to a wide variety of causes, including developmental abnormalities (e.g., amblyopia) and ocular trauma or disease (e.g., glaucoma, macular degeneration). Whether our current findings have significant functional implications for people with such binocular disorders is unclear. However, given evidence that adult patients with the three disorders specifically mentioned above exhibit prolonged reaction times, compared to age-matched visually-normal subjects, when preparing to overtly grasp real 3D objects (Grant et al., 2007; Kotecha et al., 2009; Pardhan et al., 2012), it is conceivable that impaired motor planning evoked by the object’s affordances contributes to their delayed movement onsets. Further research is planned to validate and expand upon these insights.

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Appendix A

List of the objects used to form the prime stimulus set in Experiments 1 and 2

Graspable objects	Pinchable objects
Glass	Key
Screwdriver	Lighter
Mug	Rubber
Knife	Small highlighter
Deodorant can	Battery
Tea-box	Safety razor cover

Table 1. Mean percentage error rates in Experiment 1 (SDs shown in brackets)

Monocular vision

Object type	Power-grip response	Precision-grip response
Graspable object	*5.3 (6.2)*	*3.4 (4.3)*
Pinchable object	*6.5 (5.5)*	*5.6 (5.4)*

Binocular vision

Object type	Power-grip response	Precision-grip response
Graspable object	*4.3 (4.9)*	*4.7 (4.8)*
Pinchable object	*5.9 (5.2)*	*3.7 (5.0)*

Figure legends

Figure 1

Sequence of presentation in a typical RT trial for Experiment 1. A binocular vision / power-grip object prime trial is depicted.

Figure 2

Means of median response times for all experimental conditions in Experiment 1. Error bars denote standard errors.

Figure 3

Sequence of presentation in a typical TMS trial from Experiment 2. A precision-grip object prime trial is depicted.

Figure 4

Means of median peak-to-peak MEP sizes for all conditions from Experiment 2. Error bars denote standard errors.