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Objects rapidly prime the motor system when located near the dominant hand

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Abstract

Objects are said to automatically “afford” various actions depending upon the motor repertoire of the actor. Such affordances play a part in how we prepare to handle or manipulate tools and other objects. Evidence obtained through fMRI, EEG and TMS has proven that this is the case but, as yet, the temporal evolution of affordances has not been fully investigated. The aim here was to further explore the timing of evoked motor activity using visual stimuli tailored to drive the motor system. Therefore, we presented three kinds of stimuli in stereoscopic depth; whole hand grasp objects which afforded a power-grip, pinch-grip objects which afforded a thumb and forefinger precision-grip and an empty desk, affording no action. In order to vary functional motor priming while keeping visual stimulation identical, participants adopted one of two postures, with either the dominant or non-dominant hand forward. EEG data from 29 neurologically healthy subjects were analysed for the N1 evoked potential, observed in visual discrimination tasks, and for the N2 ERP component, previously shown to correlate with affordances (Proverbio, A.M., Adorni, R., D’Aniello, G.E., 2011. 250 ms to code for action affordance during observation of manipulable objects. Neuropsychologia 49, 2711–2717). We observed a link between ERPs, previously considered to reflect motor priming, and the positioning of the dominant hand. A significant interaction was detected in the left-hemisphere N2 between the participants’ posture and the object category they viewed. These results indicate strong affordance-related activity around 300ms after stimulus presentation, particularly when the dominant hand can easily reach an object.

Keywords

EEG; motor priming; dominant hand

1. Introduction

The term affordance was first introduced by JJ Gibson in 1977 who suggested that just by viewing an object we perceive how to use it. In recent years it has often been used to describe the idea that even when there is no intention to act, the intrinsic properties of an object will potentiate motor planning. This has prompted many studies investigating the existence of affordances (i.e. automatic priming of the motor system by viewed objects) in both human and non-human primates (e.g. Grezes et al. 2003; Murata et al. 1997; Rice et al. 2007; Tucker & Ellis 1998; Tucker & Ellis 2001; Valyear et al. 2007).

For example, Murata et al. (1997) took recordings from individual neurons in the ventral pre-motor area F5 of a macaque monkey. The animal was trained to observe physical objects and, on some trials only, was expected to pick up the object. 49 neurons were found to be task-related. 25 of these were described as motor neurons and the other 24 as visuomotor neurons. All 49 discharged when the monkey picked up an object. Interestingly, though, the 24 visuomotor neurons also discharged when the animal viewed objects whether or not it was a ‘pick-up’ trial. Some of these individual neurons also showed selectivity for a small set of similar objects by discharging at a higher rate when these objects were viewed. It was concluded that the visuomotor neurons were responding to the visual features of each object, reaffirming the theory that intrinsic visual properties potentiate motor planning.

Corresponding work with humans has led to much discussion as to which brain regions are similarly activated during passive object viewing. Many human studies that require a motor response focus on conflict in motor planning (e.g. Grezes et al. 2003; Tucker & Ellis 1998; Tucker & Ellis 2001; Valyear et al. 2007). This has sometimes been combined with neuroimaging. For instance, in a functional magnetic resonance imaging (fMRI) congruency task, Grèzes et al. (2003) required participants to make a precision (i.e. forefinger and thumb pinch) grip when viewing any natural object and a power (i.e. whole-hand grasp) grip when viewing any man-made object. Visual stimuli could be either congruent or incongruent for the required type of response. For example, a grape (natural, hence instructing a pinch response) would be in line with a congruent response, because the response matched the motor priming properties of the object, while a cucumber would be incongruent in this respect. Equally, for man-made objects (instructing a grasp response), a hammer was congruent while a screw was incongruent. Grèzes' group found that reaction times were greater for incongruent trials, presumably due to conflict between the action afforded by the object and the response required for the task. Correspondingly, fMRI activity in various brain regions also differed between the congruent and incongruent trials with most activation occurring in the left hemisphere. Areas correlating with the behavioural results were, in particular, the premotor cortex and also the inferior frontal sulcus, superior temporal sulcus, anterior parietal cortex and superior parietal lobe.

Interestingly, significant fMRI activity has also been observed in the right hemisphere of healthy right-handed volunteers in another type of response task (Rice et al. 2007). Here, graspable or non-graspable objects were shown orientated to either the left or to the right. After a brief mask stimulus the object was shown again, on some trials with the same orientation and on others with the opposite orientation. Subjects had to respond by pressing one button for same and another for different orientations. In this study fMRI activity was contrasted between repeated and flipped stimuli (using a form of fMRI adaptation) and revealed that the right lateral occipital-parietal junction was selective for orientation but only for graspable objects.

These and many similar findings (e.g. Goslin et al. 2012; Righi et al. 2014; Tucker & Ellis 1998; Tucker & Ellis 2001) suggest that affordances exist in humans. However, although spatially informative, the temporal resolution of fMRI is less impressive due to the signal delay of the blood oxygen level-dependent (BOLD) response. Hence the exact timing of neuronal activity caused by affordance cannot be deduced from fMRI. Recently there have been several transcranial magnetic stimulation (TMS) experiments (Buccino et al. 2009; Cardellicchio et al. 2011; Makris et al. 2011; Makris et al. 2013) which have contributed to a better understanding of the temporal evolution of affordances. For example, Buccino et al. (2009) stimulated left motor cortex, and showed greater motor evoked potentials (MEPs) 200 ms after the onset of objects with handles orientated towards the right than the left and, particularly, that these MEPs were larger for whole handles rather than damaged ones. Makris et al. (2011, 2013) presented objects affording either a precision or power grip, and found modulation in MEPs from the congruent hand muscle groups (consistent with the presence of an affordance) that began 150-300 ms after stimulus onset and died away at around 600 ms after stimulus onset.

Some recent electroencephalographic (EEG) studies have also sought to measure the timing of affordances by comparing responses to pictures of tools with non-tools (Proverbio et al. 2011; Proverbio 2012). Proverbio et al. (2011) found significantly greater anterior left hemispheric negativity for the N2 component of the event-related potential (ERP) while viewing tools compared to non-tools. The N2 is the second negative component after stimulus onset and has been associated with motor facilitation (Allami et al. 2014). Using 128 electrodes, Proverbio et al. computed the N2 from electrode sites AF3, AF4, AFP3h and AFP4h. Their time window was from 210ms to 270ms after stimulus onset. A standardized weighted low-resolution electromagnetic tomography (swLORETA) inverse solution was computed to understand the source of this increased activity for tools. In response to tools it revealed more left than right hemispheric pre-motor activity (Brodmann Area 6), as well as unilateral (left hemisphere) activation of the somatosensory cortex (Brodmann Area 3). The swLORETA computation showed that these areas were not involved in response to other (non-tool) objects. Two other ERP components were also investigated. These were firstly the positive component with peaks usually between 300ms and 600ms after stimulus onset (P300) and secondly a later slow positive component generally appearing between 400ms and 750ms after stimulus onset (late positivity). A greater centroparietal P300 component for tools compared to non-tools was observed between 550ms and 600ms after stimulus onset, whilst a larger late positivity amplitude for non-tools (from anterior frontal and prefrontal electrodes) occurred between 750ms and 850ms after stimulus onset. These have been related to attention for a target stimulus amongst a set of non-targets (Frodl-Bauch et al. 1999; Mugler et al. 2008; Nijboer et al. 2008) and controlled allocation of attention (Schienle et al. 2011; Schupp et al. 2000) respectively.

The defining feature of an affordance is that it represents priming of the *motor* system (regardless of the ultimate requirement to act or not). We wished to confirm the existence in the EEG of a differential motoric response to objects that prime grip actions compared to scenes without such objects. In their studies, Proverbio et al. had two stimulus categories and used pictures of objects that afforded both manual and non-manual actions (e.g. a bicycle and stairs were included in the tool category). We instead confined our object stimuli to those relating to the hand and utilised images containing stereo depth cues, which are known to support accurate goaldirected visually guided reach-to-grasp actions (e.g. Melmoth & Grant 2006; Melmoth et al. 2007; Melmoth et al. 2009). A question arises as to whether the EEG components identified by Proverbio et al. provide markers of purely motoric brain activation. In a design that simply correlates brain activity with different categories of visual stimuli it is difficult to rule out a purely visual contribution to observed differences. Hence we sought to overcome the problems raised by a reliance on comparisons between visual stimuli in two ways.

Firstly, in addition to the components identified by Proverbio et al. (2011) we also investigated purely visual discrimination as associated with the posterior N1 ERP component (Hopf et al. 2002; Mangun & Hillyard 1991; Thorpe et al. 1996; Vogel & Luck 2000). We used this component to search for any differences in the visual brain response evoked by our stimuli, hoping to rule out such effects.

Secondly, because any contrast between object and non-object stimulus categories may introduce systematic visual differences above and beyond those that were intended, we sought an additional manipulation that should modulate the creation of an affordance within the motor system. To this end, we had participants adopt one of two postures. The first, a sitting posture with the dominant hand close to 3D objects, should promote the generation of an affordance, whereas the second, with body rotated to have the dominant hand far away from the screen, should lessen any affordance (at least within the dominant left hemisphere).

In summary, here we ask whether viewing objects in 3D and manipulating the position of the dominant hand can provide compelling evidence of brain activity associated with affordances. We introduce a design in which any effects on ERPs from purely visual differences between objects can be ruled out. Our innovation is to provide identical visual stimulation in two posture conditions that vary the functional meaning of objects. We then identify interactions between posture and image category in the EEG, thereby revealing ERP components that index a fundamentally motoric priming effect.

2. Materials and Methods

2.1. Participants

Initially, 20 participants were recruited for this experiment, based on typical sample sizes for EEG experiments involving factorial designs with repeated measures. We were predicting interactions involving posture and image category. Following examination of these data, a bootstrap-based power analysis was used to determine a final sample size providing 80% power to detect any such interaction in the N2 (as that proved the most promising ERP component) based on the effect sizes present in the initial sample. As a consequence, a total of 29 participants were recruited to passively view 3D photographs of objects and of an empty desk (9 males, 20 females; mean age 28.1 years, SD 5.53 years). All had normal or corrected-to-normal vision with no history of neurological illness. All were right-handed as verified by the Edinburgh Handedness Inventory, adapted from Oldfield (1971). The study was approved by City University Ethics Committee and participants gave written consent.

2.2. Stimuli

Initially, 3D photographs were taken of 40 objects positioned on a desk in such a way that no left or right laterality could be ascertained, i.e. either photographs of objects without handles or photographs of objects with the handle positioned centrally. Viewpoint and light source remained constant across photos. To establish object categories for the experiment, 20 independent assessors rated the photos on whether they would use a pinch grip or whole hand grasp to hold the objects. The assessors used three categories; “always use this grip/grasp”, “mostly use this grip/grasp”, or “just more likely to use this grip/grasp”. A separate independent group of 10 people then rated the objects from 0 to 2 on how familiar they were, with 2 being a very familiar object. A subset of pictures was then chosen which contained good exemplars of objects affording either a precision or power grip (i.e. consistently rated “always” for the relevant grip and predominantly rated 2 on the familiarity scale). For the subsequent experiment, these stimuli were used to construct three stimulus categories. The first category contained only a single stimulus (an empty desk) while the other two showed objects located on the desk. Object categories consisted of one picture of each of five objects, which would normally be held in either a precision grip (pinch objects: tweezers, drawing pin, button, wedding ring, and paperclip) or a power grip (grasp objects: hairbrush, glass, mug without handle, liquid soap container and knife).

2.3. Design and Procedure

Participants were seated in an electrically shielded room, in front of a mounted stereoscope, approximately 45cm from a gamma-corrected CRT monitor refreshing at 109 Hz. Left-eye and right-eye images were displayed side by side, but presented only to their respective eyes via the mirror stereoscope (Stereo Aids, Australia). Initially, participants were allowed time to adjust the viewer so that they observed a single object in three dimensions. For this calibration, two objects, a ball and a sponge, were presented in alternation. These two objects became targets for a subsequent vigilance task.

For the main experiment, on each trial, two fixation dots were shown on screen for 1000ms (to maintain stereo fusion in the interval between pictures) followed by a colour photograph, also for 1000ms (see Figure 1A). The task was to passively view the pictures through a stereoscopic viewer, except that participants had to report the two target items (ball and sponge) whenever they appeared (with these trials excluded from the subsequent data analysis). In each block, there were 150 trials with photographs of the empty desk (‘no-object’ category) and 150 trials each from the two object categories (pinch objects and grasp objects) so that each individual object was viewed 30 times. For the vigilance task, the ball and sponge pictures were included in an additional 16 trials. Trials in each category and those of the vigilance task were presented in a randomised order.

There were two viewing postures. For the right-hand forward posture the right hand rested close to the screen with the body rotated approximately 45° away from the screen towards the left. The head was maintained directly facing the screen. For the left-hand forward posture the left hand rested close to the screen with the body rotated approximately 45° away from the screen towards the right. Again, the head was maintained facing directly towards the screen (see Figure 1B). The order of the first and second postures was counterbalanced across participants. For each posture a block lasted approximately 15 minutes and participants were offered a short break after 100, 200, 300 and 400 trials.

[INSERT FIGURE 1 SCHEMATIC OF METHODS HERE]

2.4. EEG measurement and analysis

A 64-channel electrode cap was fitted to the participant’s head with the ground electrode at position AFZ and the reference electrode at position FCZ. An additional vertical electro-oculogram electrode was placed below the left eye. Electrode impedance was kept below 20 k Ω and recorded at a sampling rate of 1000 Hz. Recording and pre-processing of the EEG data were performed with a BrainAmp DC amplifier and the BrainVision Recorder software (Brain Products, Herrsching, Germany).

For the ERP analysis the data were band-pass filtered offline with high-pass frequency of 0.1Hz and a low-pass frequency of 35Hz and re-referenced to linked mastoids. Data were segmented into epochs of 1500ms, from 500ms prior to stimulus onset to 1000ms after stimulus presentation. The Gratton and Coles method (Gratton et al. 1983) was used for ocular correction, and baseline correction was applied using a window from 100ms to 0ms before the stimulus. Epochs were also excluded automatically if any values exceeded a threshold of ± 100µV, resulting in a rejection rate of ~10%. Based on inspection of averaged data, peak event-related potential (ERP) amplitudes for the posterior N1 component were computed at the PO3 and PO4 electrodes and the anterior component at the F1 and F2 electrodes, both in the interval 100ms to 200ms after stimulus onset. Immediately after the clearly observable N1 ERPs the EEG traces varied considerably in the different stimuli categories and across participants. Consequently, for the anterior N2 component at the F1 and F2 electrodes a peak-to-peak measurement was taken from the most positive preceding peak (P2) to the most negative following peak (N2). The P2 was calculated as the local peak between 160ms and 260ms after stimulus onset and the N2 was calculated as the local peak between 235ms and 360ms after stimulus onset. For each individual participant’s set of data an earlier P2 peak corresponded with an earlier N2 peak and a later P2 peak corresponded with a later N2 peak. The aim was to standardize the measurement between categories by observing the amplitude between the peaks.

Repeated measures 2x2x3 ANOVAs were carried out assessing differences in N1 and N2 amplitudes with the following within-subject factors: posture (left and right-hand forward), hemisphere (left and right) and the three stimulus categories (whole-hand grasp objects, pinch-grip objects and no object). The Greenhouse-Geisser correction was used to correct for violations of sphericity.

3. Results

Our analyses focused on both the prominent N1 negative component, whose time-course varies across the scalp from anterior to posterior, and the anterior N2, described by Proverbio et al. (2011) and previously inferred to reflect the presence or absence of an affordance.

3.1. The N1 component

We observed a distinct N1 component. At posterior sites, PO3 and PO4, (not shown) the posture by hemisphere by stimulus category (2x2x3) ANOVA revealed no difference between postures, nor between hemispheres, nor stimulus categories and there were no significant interactions. In fact, F<1.0 for all effects involving stimulus categories.[1] Mean microvolt stimulus category differences were: between whole-hand grasp and pinch-grip 0.39µV (SD = 2.30), between whole-hand grasp and no object 0.14µV (SD = 2.51) and between pinch-grip and no object 0.53µV (SD = 1.51).

At anterior sites, namely electrodes F1 and F2, (see Figure 2, earlier greyed region) the posture by hemisphere by stimulus category (2x2x3) ANOVA revealed a main effect of hemisphere F (1, 28) = 9.023; p = .006, ηp^2 = .244 and a main effect of stimulus category F (2, 56) = 4.949; p = .020, ηp^2 = .150. T-tests showed no significant differences between whole hand grasp objects and pinch-grip objects, p =

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[1] Actual means, 1.16µV (SD = 3.88) for the whole-hand grasp object, 1.55µV (SD = 2.64) for the pinch-grip object and 1.01µV (SD = 2.38) for no object.

1.00, and no differences between grasp objects and the empty desk, p = .254. There was, however, a significant difference between pinch-grip objects and empty desk, p = .001. There was no main effect of posture. There was also a significant interaction between posture and hemisphere F (1, 28) = 7.032; p = .013, ηp² = .201; pairwise follow-ups showed significant differences between hemispheres only in the right-hand forward posture, p = .001. All other interactions involving stimulus categories, were not significant: posture x hemisphere x stimulus category, p = .329; posture x stimulus category, p = .337; hemisphere x stimulus category, p = .234.

3.2. The N2 component

Turning to the N2 ERP component: As can be seen in Figure 2 (later greyed region), for posture 1 (i.e. right hand forward) there is an enhanced N2 in both object categories compared to the no-object category. This difference between categories is far less pronounced in posture 2, particularly in the left hemisphere. A posture by hemisphere by stimulus category (2x2x3) ANOVA showed significant main effects of hemisphere, F (1, 28) = 9.918; p = .004, ηp² = .262, and stimulus category, F (2, 56) = 24.091; p < .001, ηp² = .462. All t-tests between stimulus categories showed significance; p = .026 between whole-hand grasp objects and pinch-grip objects while p < .001 between each object category and the empty desk.

Of particular interest for our design, the interaction between posture, hemisphere and stimulus category was marginally significant, F (2, 56) = 2.936; p = .081, ηp² = .095. However, we had a clear directional prediction regarding this interaction (that the posture by stimulus category interaction should be enhanced in the left hemisphere), which was supported by the pattern of means (see Figure 2). Although F tests are strictly speaking one-tailed, an ANOVA interaction can be considered a form of “multi-tailed” test, as no directionality of effect is specified (see Howell, 1997, pg. 154, for this argument in the context of another multi-tailed test, the χ^2 test of association). With under half of all possible interaction data patterns conforming to our a priori expectation, we felt justified in using an alpha value of 0.1. Hence, we considered the interaction between posture, hemisphere and stimulus categories meaningful, and a further posture by stimulus category (2x3) ANOVA was conducted separately for each hemisphere in order to follow it up.

For both hemispheres the difference between stimulus categories was significant (right hemisphere, F (2, 56) = 24.229; $p < .001$, ηp² = .464; left hemisphere, F (2, 56) = 21.769; $p < .001$, ηp² = .437). For the right hemisphere (F2 electrode) the posture by stimulus category interaction was not significant; p = .285. Critically, for the left hemisphere (F1 electrode) there was a significant interaction between posture and stimulus category, F (2, 56) = 3.201; p = .048, ηp² = .103. The interaction reflected a greater modulation of the N2 by object condition for the right-hand forward posture than for the left-hand forward posture and pairwise follow-ups showed that both of the object categories differed from each other, p = .001 and both object categories differed from the no object category $p < .001$ in the right-hand forward posture. However in the left-hand forward posture there was less overall modulation by object category (driving the interaction effect in the posture by stimulus category ANOVA); while both object categories still differed from the no object category $p < .001$, there was no significant difference between the two types of object categories, p = .318.

[INSERT FIGURE 2 ELECTRODE TRACES HERE]

3.3. Other ERP components

Proverbio et al. (2011) additionally observed a peak between 750ms and 850ms over prefrontal sites which they described as late positivity and which produced a significantly larger amplitude for non-tools compared to tools. In addition, the P300 ERP over centro-partietal electrodes also produced significantly larger amplitudes for tools compared to non-tools. We also sought these effects. However, no discernible ERP was found near 800ms. For the P300 ERP, recordings from C1, C2, CP1 and CP2 electrodes were analysed as these corresponded most closely with the CCP1h, CCp2h electrodes used by Proverbio et al. (2011). Their P300 component was found between 550ms and 600ms, but observing our EEG data, the component was not clearly discernible, so we did not investigate further.

4. Discussion

This experiment sought to provide further ERP evidence regarding the timing of affordances, by manipulating participants’ posture in relation to the objects being viewed. We presented participants with either whole-hand grasp or pinch-grip objects on a desk, or with an empty desk, and positioned their bodies so as to vary whether those objects could be reached easily with the dominant hand (while holding visual stimulation constant). We then recorded brain activity while they observed a random sequence of stimuli at a rate of 0.5 Hz. We also addressed the functional relevance of motor primes more generally in our experiment by providing stereo depth cues, and demonstrated a robust affordance-based brain response under these conditions (c.f. Makris et al., 2013).

The resulting significant interaction between posture and stimulus category, found in the dominant left-hemisphere N2 ERP component of right-handed participants, demonstrates that the N2 reflects object affordances, which should be affected specifically by the participants’ position in relation to the stimuli. Indeed, the N2 component even appeared to distinguish between the types of grasp or grip that would be appropriate for the particular object being presented (rather than simply distinguishing between graspable objects and empty desks). The affordance effect was present in the left-hand forward posture, but to a lesser extent as differences were found only between objects (of either type) and the empty desk. Although there was a significant effect for stimulus category in the right hemisphere, there was no significant interaction between posture and stimulus category like the one obtained in the left hemisphere. It might have been expected that in the right hemisphere the N2 component would be significantly greater in the left hand forward posture. However, as our participants all had right hand dominance, these results substantiate our theory that it is the dominant hand positioned close to an object that enhances affordance effects.

Our results complement and extend those of Proverbio et al. (2011) and Proverbio (2012) who investigated EEG markers for automatic object-action priming. In their work, pictures of objects affording action were contrasted with pictures that did not afford any actions, and effects were found in the N2 (and later), with a swLORETA analysis linking this effect to motor regions of the brain.

Our posture manipulation changed the functional relevance of objects without changing their visual properties, and thus our data strengthen their finding. If significant differences had simply been shown between the object conditions, it might be argued that the gross visual differences between a large, graspable object, a small, pinchable object and an empty desk, could account for the ERP differences without implying that functional, motor properties of objects were the primary cause.

In addition to ruling out visual effects via the logic of our design, we also strengthened our inference of a motoric effect by observing the visual N1 ERP component between 100ms and 200ms after stimulus onset. Interestingly, for both postures, at the posterior PO3 and PO4 electrodes, the N1 ERP component had a very similar peak voltage at very similar latencies for all stimulus categories – whole hand grasp objects, pinch-grip objects and no object. Hence, in our data, there appears to be little detectable difference between stimulus-evoked visual activity in parietal-occipital regions between 100ms and 200ms after stimuli onset. However, anteriorly (at the F1 and F2 electrodes) this component did show differences in peak values between the stimulus categories. For both hemispheres, pinch-grip objects produced a significantly greater negative peak than the empty desk. The N1 peak produced by the whole-hand grasp objects was also larger (althought not significantly) than that produced by the empty desk (see Figure 2).

These findings may be due to early motoric discrimination of picture content. Evidence from previous experiments suggests that the anterior N1 is produced by motor responses (Vogel & Luck 2000). In their study, a first experiment incorporated a button press response while the second asked participants to just keep a count of the number of stimuli presented. In the first experiment a large anterior N1 effect was observed. In the second, this effect was diminished. The researchers hypothesised that the anterior N1 ERP in the first experiment was due to an overlap of preparation for a motor response with the stimulus-elicited response. As a footnote in the article, Vogel and Luck confirmed completion of further experiments to control for motor-related overlap. In one they instructed participants to respond at the same speed for simple and complex tasks and in the other the SOA was varied to reduce anticipated motor responses. In both of these the anterior N1 was eliminated but the posterior N1 remained. Thus prior research would suggest that while posterior N1 activity relates to purely visual properties, the anterior N1 is influenced by motor preparation.

It is therefore striking that in our experiment, we observed essentially no anterior N1 for an empty desk, with this component emerging only when objects were viewed despite no requirement to actually respond to them. This is a very early ERP component and therefore it is possible that full affordance properties have yet to be completely processed. Indeed, there was a (non-significant) trend towards an interaction between stimulus category and posture even in the anterior N1. In our experiment the subsequent N2 component, particularly the significant left-hemisphere interaction between posture and stimulus category, serves to confirm motoric involvement and, consequently, the presence of an affordance.

Ours is the first EEG study to evidence affordances via changes in the functional relevance of graspable objects. In a recent TMS study a computer generated 3D room was used (presented on a 2D display without stereo depth; Cardellicchio et al. 2011) to vary whether stimuli could be reached or not. The stimuli consisted of either a mug with a handle (graspable object) or a cube (non-graspable object) on a table. TMS pulses were delivered to obtain responses from the first dorsal interosseous and the opponens pollicis hand muscles, both of which are activated when grasping a mug handle. The mug and the cube were shown separately in two conditions. Each was shown positioned within reachable space and also further away, in non-reachable space. Electromyographic (EMG) recordings showed that when it was observed within reachable space, the mug produced significantly greater MEPs than when it was observed in non-reachable space. No such effect occurred with the cube stimulus. From this result, the authors suggested that the affording properties of an object are able to induce motor representations only when the object is appropriately positioned within the observer’s reach.

In the current study, while each 3D object appeared in exactly the same spatial position, the posture of the observer was altered, effectively placing either the dominant (right) hand closer to the object (Posture 1) or the non-dominant (left) hand closer (Posture 2). Lateralized affordance bias from the objects themselves was eliminated as the objects were displayed with any handles presented centrally. Our results, showing a greater N2 ERP component for object stimuli compared to the empty desk, but particularly when the object could be manipulated with the dominant hand, corroborate and advance those of Cardellicchio et al. (2011). Although the objects were all effectively positioned within reachable space, the results relate enhanced affordance properties particularly to the close proximity of the dominant hand. This early affordance effect also conforms with other studies showing greater MEP sizes around 200ms after stimulus onset when assessed via handle orientation (Buccino et al. 2009) and at 300ms after stimulus onset (but not later) when assessed via grip congruence (Makris et al. 2011; Makris et al. 2013).

Our result is at odds with some previous findings, e.g. Wilf et al. (2013). This group sought to dissociate affordance effects and spatial effects (Simon 1969) and determine whether there was an interaction between them. Their stimuli were pictures of graspable and non-graspable objects projected to either the left or right side at around shoulder height. The sizes and spatial properties of the images were matched, e.g. an elephant and a mug were depicted as the same size and had similar outline shapes. The task was to make a lateralised response to determine if the objects contained metal, irrespective of whether they could be grasped, for example, a right-hand response for metal and a left hand for non-metal or vice versa. Wilf et al. analysed muscle activity and obtained both an effect of spatial compatibility (i.e. enhanced left-hand responses for objects on the left and vice versa) and an effect of affordance (i.e. enhanced responses for graspable objects). Importantly, there was no interaction between spatial compatibility and affordance, implying that the latter effect emerged for objects both near and far from the responding hand. However, it is worth noting that their manipulation of object position would still have left objects reachable with either hand in relative comfort. By contrast, our posture manipulation may have been more effective in modulating action tendencies for the dominant hand as it would have required considerably more effort if participants had been required to act with the more distant hand.

Conclusion

Passively observing manipulable objects from different postures modulates EEG activity in a manner consistent with the existence of automatic affordances within the motor system. Here we have shown that, across the three stimulus categories, the evoked ERP N2 component modulates differently between participants' postures, i.e. depending upon whether the dominant or non-dominant hand was closer to the object. We have shown that this is not purely a visual effect, both through the logic of our design and by our examination of the N1 component. Prior research has suggested that the anterior N1 component is enhanced by motor preparation. As only objects requiring a power or precision grip produced the N1 component at anterior sites and the empty desk did not, this result also provides suggestive new evidence for affordance. Hence we propose that affordances generated by 3D objects may become active within 300ms after stimulus onset, consistent with other evidence from EEG and TMS experiments.

Conflict of interest statement

None declared.

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Figure Legends

Figure 1. Schematic of Experimental Methods. **A.** Example trial from the EEG paradigm. Here a whole-hand grasp object is displayed (both in stereo, as presented, and as perceived through the stereoscopic viewer, with left and right images fused). **B.** Schematic showing Posture 1 with right (dominant) hand closer to the screen and Posture 2 with left hand closer to the screen; in each case the head is maintained directly facing the screen.

Figure 2. Grand averaged F1 and F2 electrode traces for both Posture 1 (right hand forward) and Posture 2 (left hand forward). Shown in grey shaded areas are the N1 component between 100ms and 200ms after stimuli onset and the N2 component between 235ms and 360ms after stimuli onset. ERPs are depicted by a broken black line for whole-hand grasp objects, a blue line for pinch-grip objects and an orange line for the empty desk (no object). Head maps show voltage across the scalp, with greatest negativity in blue, and relate to grasp objects in Posture 1.

Figure 1

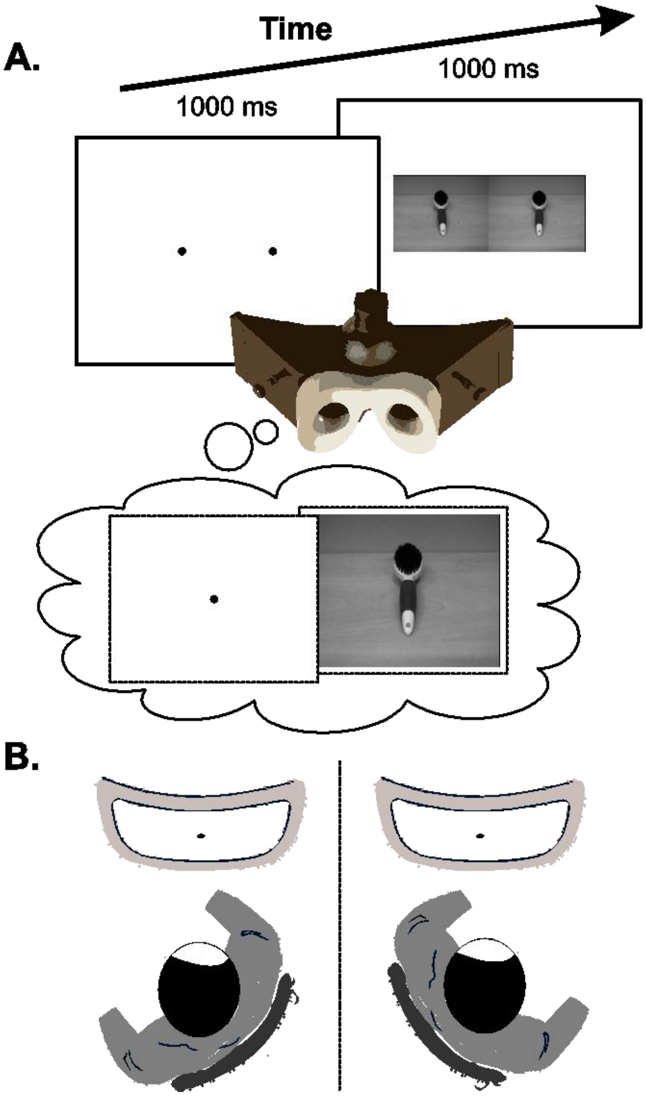
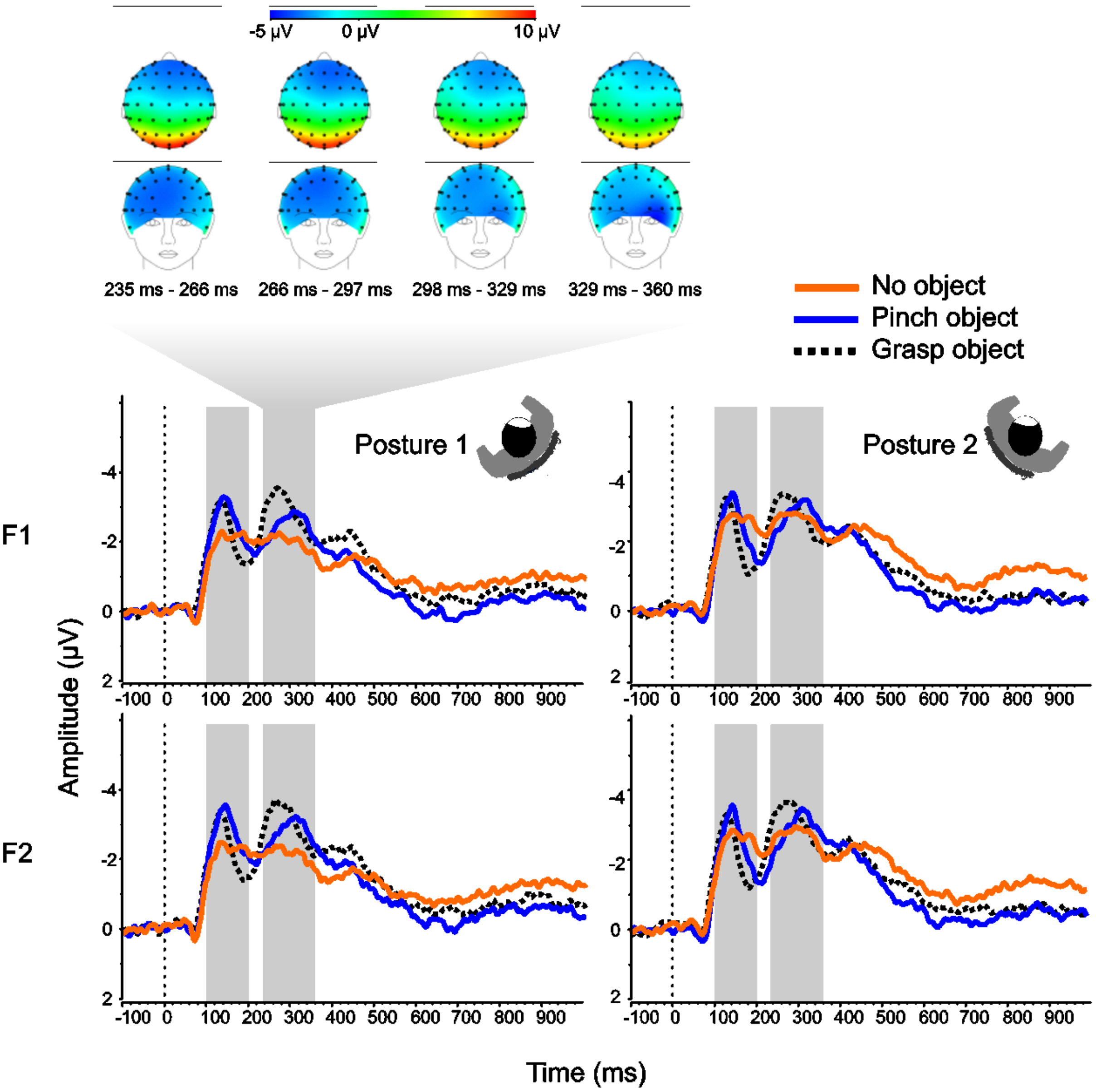


Figure 2



-5 µV
0 µV
10 µV
235 ms - 266 ms
266 ms - 297 ms
298 ms - 329 ms
329 ms - 360 ms
No object
Pinch object
Grasp object
Posture 1
Posture 2
F1
F2
Amplitude (µV)
-4
-2
0
2
-100
0
100
200
300
400
500
600
700
800
900
Time (ms)