



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, Adorni, & D’Aniello, 2011). 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 300 ms after stimulus presentation, particularly when the dominant hand can easily reach an object.

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1. Introduction

The term affordance was first introduced by 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, Tucker, Armony, Ellis, & Passingham, 2003; Murata et al., 1997; Rice, Valyear, Goodale, Milner, & Culham, 2007; Tucker & Ellis, 1998; Tucker & Ellis, 2001; Valyear, Cavina-Pratesi, Stiglick, & Culham, 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 neu-

rons 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, 2001; Valyear et al., 2007). This has sometimes been combined with neuroimaging. For instance, in a functional magnetic resonance imaging (fMRI) congruency task, Grezes 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

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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, Dixon, Fischer, Cangelosi, & Ellis, 2012; Righi, Orlando, & Marzi, 2014; Tucker & Ellis, 1998, 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, Sato, Cattaneo, Rodà, & Riggio, 2009; Cardellicchio, Sinigaglia, & Costantini, 2011; Makris, Hadar, & Yarrow, 2011; Makris, Hadar, & Yarrow, 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) and Makris et al. (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, 2012; Proverbio, Adorni, & D'Aniello, 2011). 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 210 ms to 270 ms 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 300 ms and 600 ms after stimulus onset (P300) and secondly a later slow positive component generally appearing between 400 ms and 750 ms after stimulus onset (late positivity). A greater centroparietal P300 component for tools compared to non-tools was observed between 550 ms and 600 ms after stimulus onset, whilst a larger late positivity amplitude for non-tools (from anterior frontal and prefrontal electrodes) occurred between 750 ms and 850 ms after stimulus onset. These have been related to attention for a target stimulus amongst a set of non-targets (Frodil-Bauch, Bottlender, & Hegerl, 1999; Mugler et al., 2008; Nijboer et al., 2008) and controlled allocation of attention (Schienle, Köchel, & Leutgeb, 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 goal-directed visually guided reach-to-grasp actions (e.g. Melmoth, Finlay, Morgan, & Grant, 2009; Melmoth & Grant, 2006; Melmoth, Storoni, Todd, Finlay, & Grant, 2007). 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, Vogel, Woodman, Heinze, & Luck, 2002; Mangun & Hillyard, 1991; Thorpe, Fize, & Marlot, 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.

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