

The Anterior Temporal Cortex in Action

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Abstract

Intelligent manipulation of handheld tools marks a major discontinuity between humans and our closest ancestors. Here we identified neural representations about how tools are typically manipulated within left anterior temporal cortex, by shifting a searchlight classifier through whole-brain real action fMRI data when participants grasped 3D-printed tools in ways considered typical for use (i.e., by their handle). These neural representations were automatically evoked as task performance did not require semantic processing. In fact, findings from a behavioural motion-capture experiment confirmed that actions with tools (relative to non-tool) incurred additional processing costs, as would be suspected if semantic areas are being automatically engaged. These results substantiate theories of semantic cognition that claim the anterior temporal cortex combines sensorimotor and semantic content for advanced behaviours like tool manipulation.

Introduction

The human ability to use tools (like using a knife for cutting) symbolises a great step in our evolutionary lineage (Ambrose, 2001), but the brain mechanisms underpinning this behaviour remain debated. Over the past decades, theoretical models (Lewis, 2006; Osiurak & Badets, 2016; Buxbaum, 2017) and neuroimaging evidence converge to propose that intelligent tool-use is the result of functionally interacting neural systems (for recent summaries see Garcea et al., 2014; Reynaud et al., 2016). One such neural system is the posterior parietal sensorimotor circuit proposed to perform conceptual processing about the objects during sensing and handling by cognitive embodiment theories (Allport, 1985; Mahon & Caramazza, 2008; Martin, 2016). The classic dual visual stream theory (Milner & Goodale, 1995) further incorporates visual ventrally located brain areas (e.g., Lateral Occipital Temporal Cortex) for perceiving tool properties (e.g., visual form, shape; Lingnau & Downing, 2015). Additional dual stream models describe the Inferior Parietal Lobule (IPL) and posterior Middle Temporal Gyrus (MTG) as neural sites that integrate information from sensorimotor and perceptual brain regions into a visuo-kinesthetic format relevant for tool manipulation (Rizzolatti & Matelli, 2003; Osiurak & Badets, 2016; Buxbaum, 2017). Most recently, focus has shifted toward the role of the anterior temporal cortex in tool-use (e.g., Lesourd et al., 2021), based on claims from semantic models that this area constitutes an amodal hub which weaves abstract conceptual representations (Lambon Ralph et al., 2017; Jefferies et al., 2020).

Each of these 'tool-use' brain regions have been identified by seminal picture-viewing neuroimaging studies (e.g., Chao et al. 1999). The involvement of posterior/inferior parietal and lateral occipital cortices initially suggested to code tool-related information by picture viewing studies has since been replicated by a small number of functional MRI (fMRI) experiments involving real tool manipulation (Valyear et al., 2012; Gallivan et al., 2013; Brandi et al., 2014; Styrkowiec et al., 2019; Knights et al., 2021; see Valyear et al. 2016 for a review). The anterior temporal cortex, however, has yet to be identified with real action tasks during which participants are asked to manipulate tools with their hands. This is at odds with traditional neuropsychology evidence showing that anterior temporal lobe degeneration in semantic dementia patients causes the loss of conceptual knowledge about everyday objects, despite retained shape

processing and praxis (Hodges et al., 1992; Mummery et al., 2000). In fact, converging neuroimaging evidence shows that anterior temporal cortex represents conceptual information about tools, like the usual locations or functions associated with a tool, but these findings are restricted to high-level cognitive tasks thought to rely on mechanisms distinct from real hand-tool manipulation (Goldenberg, 2017; Snow & Culham, 2021), such as picture recognition, language or pantomime (Kaleneine et al., 2009; Peelen & Caramazza, 2012; Ishibashi et al., 2018; Ishibashi et al., 2011; Marstaller et al., 2018; Chen et al., 2016).

Here, we applied whole-brain searchlights to an fMRI dataset where humans performed real hand actions with 3D-printed tools with their right-hand that were considered typical for tool-use (grasped by the handle) or not (grasped by the tool-head; Figure 1A/1C; re-analysis of Knights et al., 2021). By including biomechanically matched actions with control non-tools (grasping right vs. left) we could test which brain regions specifically contained multivariate representations about the typicality of tool actions (like grasping a spoon by its handle) independently of kinematic differences between typical and atypical actions. In fact, in a control behavioural experiment, we examined if these tool and non-tool actions were appropriately matched for biomechanics by recording hand kinematic using high-resolution motion-capture during the same paradigm outside the MR environment (Figure 1B).

Results

Real Action fMRI Experiment

Whole-brain searchlight Multivoxel Pattern Analysis (MVPA) (Figure 2A) (Kriegeskorte et al 2006; Smith & Goodale 2015) was used to identify the brain regions that represented how to appropriately grasp tools for use (i.e., by handle rather than tool-head). Specifically, a stringent typicality difference map (Figure 2) was generated using a searchlight subtraction analysis that controlled for low-level hand kinematics: the multivariate decoding map of right vs. left grasps of control non-tools was subtracted from the decoding map of typical (right) vs. atypical (left) grasps of tools (see Methods). This difference map thus reveals which brain areas contain information about how to grasp tools correctly for subsequent use, independently of low-level differences between right vs. leftward grasping movements.

As presented in Figure 2, significantly higher decoding accuracy for tools than non-tools was observed in a large cluster (see Table 1 for cluster sizes) comprising an anterior portion of the left Superior and Middle Temporal Gyri (STG; MTG) that extended into the Parahippocampal Gyrus (PHG). Other clusters surviving correction for multiple comparisons included those within the right Fusiform Gyrus (FG) and anterior Superior Parieto-Occipital Cortex (aSPOC). No cluster of activity demonstrated higher decoding accuracy in the reverse direction, that is, for non-tools higher than tools.

Table 1. Searchlight result cluster sizes (voxels), peak coordinates (Talairach) & statistics.

Region	Cluster Size	X	Y	Z	t-statistic	<i>p</i>
L-MTG	1674	-39	-16	-11	5.6	<.001
L-STG		-45	-7	-5	5	<.001
L-PHG		-27	-19	-23	4.8	<.001
R-FG	1410	30	-73	-5	4.8	<.001
R-SPOC	278	15	-67	31	4.64	<.001

Behavioural Motion-Capture Experiment

To better understand action processing speed for tools vs. non-tools, we measured hand kinematics with high-resolution motion-capture while participants performed the same task outside the MRI. As presented in Figure 3, analysis of reaction time (RT) and movement time (MT) both revealed a significant main effect of object category (RT: $F(1,21) = 15$, $p = 0.001$, $\eta p^2 = 0.42$; MT: $F(1,21) = 5.74$, $p = 0.026$, $\eta p^2 = 0.22$) where grasping was slower for tools than non-tools (RT mean difference [standard error] = 9.7ms [2.5ms]; MT mean difference = 6ms [2.5ms]). Overall effects of reach direction (i.e., slower across-body reaches) were also observed where leftward (relative to rightward) actions had longer MTs ($F(1,21) = 8.9$, $p = 0.007$, $\eta p^2 = 0.3$) and a decreased peak velocity (PV) ($F(1,21) = 11.48$, $p = .003$, $\eta p^2 = 0.35$) (MT mean difference = 14.8ms [5ms]; PV mean difference = 34.4ms [10.2ms]) (Figure S1). No other significant main effects or any interaction between object category and typicality were found (all p 's > 0.15). Importantly, this lack of interaction indicates that timing did not differ specifically for grasping tools typically vs. atypically when compared to the matched movements with control non-tools.

Discussion

Our real action searchlight analysis presents the first fMRI evidence that left anterior temporal cortex is sensitive to action information about tool movements during real 3D object manipulation (Figure 2B). These results are in line with recent tool-use models (e.g., Lesourd et al., 2021) that include claims from semantic cognitive theories about the role of anterior temporal cortex in constructing abstract object representations (Schwartz et al., 2011; Lambon Ralph et al., 2017; Jefferies et al., 2020). According to these leading models, the anterior temporal cortex processes conceptual knowledge that is feature invariant (i.e., generalises across exemplar identities) like the typical way tools are handled for use (i.e., grasp tool by its handle), as demonstrated here.

Anatomically, the reported neural region peaks here are near anterior temporal lobe clusters known to code semantics during tool pantomimes (Chen et al., 2016) or tool manufacturing (Putt et al., 2017). The peak location of these regions is further along the posterior axis than reported during object knowledge association tasks (e.g., Peelen & Caramazza, 2012), but general standardised

neuropsychological tests of associative knowledge have been reported at comparable locations (e.g., Visser et al. 2012). Implementing specialised distortion correction (Embleton et al. 2010) or an increased field of view (Visser et al., 2010) will be useful for future fMRI studies to address whether areas further along the temporal pole also code information about tool manipulation. As for the left lateralisation of this effect, this resembles a popular model of the left hemisphere tool processing networks (Lewis, 2006) and is in line with the fact that all movements were performed with the right-hand during our study. Moreover, left lateralised anterior temporal responses have been reported for semantic language processing (Visser & Lambon Ralph, 2011) which, when considered alongside our results, resembles the prevalent view across philosophy (Montagu, 1976), and more recently neuroscience (e.g., Stout & Charminade, 2012; Thibault et al., 2021), that language and motor skills are tightly linked.

Remarkably, this tool-related semantic content was detectable even when task performance was independent to tool conceptual processing. That is, unlike prior tasks that have asked participants to explicitly attend to different tool associations [e.g., pantomiming actions related to scissors vs. pliers (Chen et al. 2016) or recalling if a tool is typically found in the kitchen vs. garage (Peelen & Caramazza, 2012)], our participants were simply instructed to grasp the 'left' or 'right' side of the stimuli and, throughout all aspects of experimentation (see Methods), the stimuli were purposefully referred to as 'objects' (rather than 'tools'). Since participants were not required to form intentions of using these tools, or even process their identities, our results therefore demonstrate that tool representations are automatically triggered. Like similar findings (e.g., Rizzolatti et al., 1988; Tucker & Ellis, 1998; Valyear et al., 2012), this automaticity supports influential affordance theories (Gibson, 1979; Cisek, 2007; Bach et al., 2014; Buxbaum, 2017) which predict that merely viewing objects potentiates action. Our results provide evidence of this phenomena for humans at a fine spatial resolution (e.g., compared to the Bereitschaftspotential; Shibasaki & Hallet, 2006) and during realistic object manipulation (i.e., for tool-use that are directly viewed without the use of mirrors).

Representations about actions with tools also extended into the fusiform and medial parieto-occipital cortex (Figure 2B), consistent with previous views that these areas code semantics, due to either showing crossmodal responses (e.g., reading tool words and viewing tool pictures; Devlin et al. 2005; Binder et al., 2009; Fairhall & Caramazza, 2013) or representing learnt object-associations (Liuzzi et al., 2020). In fact, our results are in line with the hub-and-spoke theory (Patterson, et al., 2007) suggesting that these two domain-general systems (e.g., for perception or action, Milner & Goodale, 2006) may act as spokes to a left anterior temporal cortex 'hub' when automatically processing learnt tool movements. Indeed, fusiform cortex is well known for processing perceptual information about object form (e.g., Kourtzi et al. 2005) whilst visuomotor computations are attributed to SPOC (e.g., Prado et al., 2005) and both regions are sensitive to prior experience, such as for processing typical action routines (Scholz et al., 2009; Rossit et al., 2013) or object functions (Weisberg et al. 2006). Alternatively, these regions could be implicated in networks supporting inference about object properties and their relationship to the laws of physics (e.g., Osiurak & Badets, 2016; Fischer et al., 2016; Schwettmann et al., 2019), though this account does not necessarily preclude a role of the anterior temporal cortex in the semantic aspects of tool-use.

Consistent with the neural differences observed by contrasting actions with tool and non-tool objects (Figure 2B), our behavioural motion-capture results similarly demonstrated slower overall responses for grasping tools than non-tools (Figure 3). From an experimental perspective, the finding of a general object category main effect independent of reach direction indicates that the biomechanics for actions involving the handle and head of the tools were appropriately matched. In other words, basic kinematic differences between different actions cannot simply explain the tool-specific decoding. Considered theoretically, the observed faster non-tool responses are consistent with many accounts describing how tool-related actions are achieved via psychological (e.g., Arbib, 1981; Rumiati & Humphreys, 1998; Christensen et al., 2019) and neural (e.g., Jeannerod et al., 1995; Milner & Goodale, 1995; 2006; Johnson-Frey, 2003; Young, 2006; Bub, Masson & Cree, 2008; Buxbaum, 2017) mechanisms that are distinct from those used for basic motor control. Similar slowing for tools has been observed in simple button-press RT experiments when comparing pictures of tools and of simple shapes (Vingerhoets et al., 2009) or other object categories (e.g., natural objects; Borghi et al., 2007). As with our findings, these simple RT effects are thought to be caused by the interference from the additional processing of competing (yet task irrelevant) functional associations that are automatically triggered by viewing tools (e.g., Cisek & Kalaska, 2010; Jax & Buxbaum, 2010).

By virtue of the grasping paradigm used here, our results are unable to capture which brain regions represent real tool-use (like scooping with a spoon). Our grasping paradigm ensured that biomechanical properties of the movements were tightly controlled across conditions (e.g., by specifying grip points), but ongoing work in our laboratory is extending these paradigms to real tool-use with more variable degrees of freedom. Further, additional functional connectivity approaches utilising Dynamic Causal Modelling (DCM) (e.g., Tak et al., 2021) will be suited to deepen our understanding of the relationship between the anterior temporal cortex and other systems proposed to support tool-use. For example, DCM could be used to determine whether, as predicted by hub-and-spoke theory (Lambon Ralph, Jefferies, Patterson & Rogers, 2017) left anterior temporal cortex influences ventral visual stream activity in a bidirectional manner.

Altogether, neural representations were detected for the first time in anterior temporal areas that leading theories of semantic cognition claim to build rich amodal relationships about objects and their uses. By observing the automaticity of these task-irrelevant effects across both behaviour and the brain, our results begin to uncover which, as well as how, specific brain regions have evolved to support efficient tool-use, a defining feature of our species.

Methods

fMRI

Participants

Nineteen healthy participants (10 male; mean age = 23 +/- 4.2 years; age range, 18–34 years, described in Knights et al. (2021), performed the fMRI real action experiment, with each providing written consent in line with procedures approved by the School of Psychology Ethics Committee at the University of East Anglia.

Apparatus & Stimuli

The 3D-printed kitchen tool and biomechanically matched non-tool bar objects were adapted from Brandi et al. (2014) (Figure 1A). As in Knights et al. (2021), the dimensions of each non-tool were matched to one of the tools, such that variability was minimized and kinematic requirements were as similar as possible between different grasps (i.e., left vs right and small vs large), including controlling for low-level shape features that can confound tool-effects, like elongation (Sakuraba et al., 2012). The MR-compatible turntable apparatus used to present the 3D objects (Figure 1A) and its setup are described in Knights et al. (2021), including the use of an upper-arm restraint and industry standard cushioning to minimise the risk of motion artefacts.

Experimental design

A powerful block-design fMRI paradigm (Knights et al. 2021) maximised the contrast-to-noise ratio, to generate reliable estimates of average voxel response patterns (Fig. 1C), while also improving the detection of blood oxygenation level-dependent (BOLD) signal changes without significant interference from artefacts during overt movement (Birn et al., 2004). Briefly, a block began with an auditory instruction ('Left' or 'Right') and participants grasped the object during 10 second ON-block when the object was briefly illuminated using a right-handed precision grip (i.e., index finger and thumb) along the vertical axis. Throughout experimentation (i.e., consent materials, training instructions) the stimuli were referred to as 'objects' such that participants were naïve to the study's purpose of examining typical versus atypical tool actions.

Acquisition

The BOLD fMRI measurements were acquired using a 3T wide bore GE-750 Discovery MR scanner. To achieve a good signal to noise ratio during the real action fMRI experiment, the posterior half of a 21-channel receive-only coil was tilted and a 16-channel receive-only flex coil was suspended over the anterior-superior part of the skull (see Fig. 1B). A T1-weighted (T1w) anatomical image was acquired with BRAVO sequences, followed by T2*-weighted single-shot gradient Echo-Planer Imaging (EPI) sequences for each block of the real action experiment, using standard parameters for whole-brain coverage (see Knights et al., 2021).

Data Preprocessing

Preprocessing of the raw functional datasets and ROI definitions were performed using BrainVoyager QX [version 2.8.2] (Brain Innovation, Maastricht, The Netherlands). Anatomical data were transformed to Talairach space and fMRI time series were pre-processed using standard parameters (no smoothing) before being coaligned to an anatomical dataset (see Knights et al., 2021). For each block of interest, and each single run independently, the timeseries were subjected to a general linear model with predictors per condition of interest, as to estimate activity patterns for searchlight MVPA (6 tool and 6 non-tools blocks per run). A small number of runs with movement or eye errors were removed from further analysis (see Knights et al., 2021).

Searchlight Pattern Classification

Searchlight MVPA (Kriegeskorte et al., 2006) was performed independently, per participant, for tool and non-tool trial types using separate linear pattern classifiers (linear support vector machines) that were trained to learn the mapping between a set of brain-activity patterns (β values computed from single blocks of activity) and the type of grasp being performed with the tools (typical vs atypical) or non-tools (right vs left). A cube mask (5 x 5 x 5 voxel length, equal to 125 voxels) was shifted through the entire brain volume, applying the classification procedure at each centre voxel (Smith & Goodale, 2015) to measure the accuracy that a given cluster of activity patterns could be used to discriminate between the different tool, or non-tool, actions.

To test the performance of our classifiers, decoding accuracy was assessed using an n-fold leave-one-run-out cross-validation procedure; thus, our models were built from $n - 1$ runs and were tested on the independent n th run (repeated for the n different possible partitions of runs in this scheme; Duda et al., 2001; Smith and Muckli, 2010; Smith and Goodale, 2015; Gallivan et al., 2016) before averaging across n iterations to produce a representative decoding accuracy measure per participant and per voxel. Searchlight analysis space was restricted to a common group mask within Talairach space, defined by voxels with a mean BOLD signal > 100 for every participant's fMRI runs to ensure that all voxels included in searchlight MVPA contained suitable activation. Beta estimates for each voxel were normalized (separately for training and test data) within a range of -1 to 1 before input to the SVM (Chang and Lin, 2011), and the linear SVM algorithm was implemented using the default parameters provided in the LibSVM toolbox ($C = 1$). Pattern classification was performed with a combination of in-house scripts (Smith and Muckli, 2010; Smith and Goodale, 2015) implemented in Matlab using the Searchlight toolbox (Pereira & Botvinick, 2011).

Statistical Analysis

Voxel accuracies from searchlight MVPA for each participant were converted to unsmoothed statistical maps. To assess where in the brain coded information about typicality, we used a paired samples t-test approach: non-tool accuracy maps were subtracted from the tool accuracy map, producing single participant typicality difference maps (i.e., tool $>$ non-tool) where it was tested, at the group-level, whether

the difference in decoding accuracies for tools vs. non-tools was greater than zero at each voxel. The BrainVoyager cluster-level statistical threshold estimator (Goebel et al., 2006; Forman et al., 1995) was used for cluster correction (voxelwise thresholds were set to $p = 0.01$ and then the cluster-wise thresholds were set to $p < .05$ using a Monte Carlo simulation of 1000 iterations), before projecting results on to a standard surface (Xia et al., 2013).

Behavioural Control Experiment

Participants

Twenty-two right-handed (Edinburgh Handedness Questionnaire; Oldfield, 1971) healthy volunteers completed the motion-capture experiment (6 males, 19-29 years of age, mean age = 22.3, SD = 2.4). Ten participants had completed the previous fMRI experiment. All had normal or corrected-to-normal vision, no history of motor, psychiatric or neurological disorders and gave informed consent in accordance with the ethical committee at the University of East Anglia.

Apparatus & Stimuli

Stimuli were the same 3D-printed objects used in the fMRI experiment. A Qualisys Oqus (AB, Gothenberg, Sweden) sampling at 179 Hz, measured the position of small passive markers affixed to the participants' right wrist and the nails of the right index finger and thumb (Figure 1B). The MR-compatible turntable apparatus was setup in the motion-capture laboratory identically to the fMRI experiment. This included using the same distances between the resting hand and object centre (43cm) and the centrally aligned red fixation LED (subtending a mean visual angle of $\sim 20^\circ$ from the centre of stimuli), as well as requiring a comparable head tilt ($\sim 20^\circ$). The two minor differences between the MR and motion-capture environments was that for motion-capture there was no arm-strap or eye-monitoring cameras (though participants completed the same pre-experiment training and received verbal reminders between experimental blocks to maintain fixation and to minimise upper arm movements) and the use of noise cancelling headphones (Bose Corporation, USA) to ensure that the sound of stimulus placement did not provide cues about an upcoming trial.

Experimental Design

Experimental designs were almost identical across the fMRI and behavioural control experiments. The first difference was that the elements critical for modelling the haemodynamic response (baseline periods between trials) during fMRI were omitted were not carried out in this behavioural experiment: Second, an additional block was collected due to the risk of excluding trials due to marker-occlusion. On average participants completed seven runs (minimum six, maximum seven) totalling 84 experimental trials and 21 repetitions per condition per participant.

Data Preprocessing

Kinematic data were obtained by localising the x, y and z positions of the markers attached to the index finger, thumb and wrist of the participants' right hand (Figure 1B). These 3D positions were filtered using a low-pass Butterworth filter (10 Hz-cut-off, 2nd order). Wrist marker position determined movement on-offset (velocity-based criterion = 50mm/s) and, in the case that these value was never exceeded, the local minimum of the velocity trace was used as the offset of the outward reaches (Quinlan & Culham, 2015).

Trial-level reach kinematic dependent variables (Reaction Time, Movement Time, Peak Velocity and time to Peak Velocity; RT; MT; PV; tPV) were computed per the five grasping repetitions and subsequently collapsed. The grand mean, per participant, for the four conditions were retained after removing problematic trials (2.62%) based on the following cases: marker occlusion (2.09%), incorrect object presentation (0.04%) and participant responses that were extremely slow (0.11%; i.e., >1000ms) or in the wrong direction (0.38%).

Statistical Analysis

Repeated measures ANOVAs were used to compare behavioural performance across conditions in a 2 (object category: tools vs. non-tools) x 2 (typicality: typical vs. atypical) factorial design.

Data Availability

The full raw f/MRI dataset is accessible from OpenNEURO (<https://openneuro.org/datasets/ds003342/versions/1.0.0>). The motion-capture datasets are accessible from the Open Science Framework (<https://osf.io/etyqs/>).

Code Availability

Computer code for running the experiments and analysis of the fMRI (<https://osf.io/zxnpv>) and behavioural datasets are accessible from the Open Science Framework (<https://osf.io/etyqs/>).

References

- Ambrose, S. H. (2001). Paleolithic technology and human evolution. *Science*, 291(5509), 1748-1753.
- Anzellotti, S., Fairhall, S. L., & Caramazza, A. (2014). Decoding representations of face identity that are tolerant to rotation. *Cerebral Cortex*, 24(8), 1988-1995.
- Arbib, M. A. (1981). Perceptual structures and distributed motor control. In: Brooks V. B. (Ed.) *Handbook of physiology – The nervous system II, Motor control, Part 1*. American

- Bach, P., Nicholson, T., & Hudson, M. (2014). The affordance-matching hypothesis: how objects guide action understanding and prediction. *Frontiers in human neuroscience*, 8, 254.
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral cortex*, 19(12), 2767-2796.
- Birn, R. M., Cox, R. W., & Bandettini, P. A. (2004). Experimental designs and processing strategies for fMRI studies involving overt verbal responses. *Neuroimage*, 23(3), 1046-1058.
- Brandi, M. L., Wohlschläger, A., Sorg, C., & Hermsdörfer, J. (2014). The neural correlates of planning and executing actual tool use. *Journal of Neuroscience*, 34(39), 13183-13194.
- Buxbaum, L. J. (2017). Learning, remembering, and predicting how to use tools: Distributed neurocognitive mechanisms: Comment on Osiurak and Badets (2016).
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature neuroscience*, 2(10), 913-919.
- Chen, Q., Garcea, F. E., & Mahon, B. Z. (2016). The representation of object-directed action and function knowledge in the human brain. *Cerebral Cortex*, 26(4), 1609-1618.
- Christensen, W., Sutton, J., & Bicknell, K. (2019). Memory systems and the control of skilled action. *Philosophical Psychology*, 32(5), 692-718.
- Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362 (1485), 1585-1599.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, 33, 269-298
- Devlin, J. T., Rushworth, M. F., & Matthews, P. M. (2005). Category-related activation for written words in the posterior fusiform is task specific. *Neuropsychologia*, 43(1), 69-74.
- Fairhall, S. L., & Caramazza, A. (2013). Brain regions that represent amodal conceptual knowledge. *Journal of Neuroscience*, 33(25), 10552-10558.
- Fischer, J., Mikhael, J. G., Tenenbaum, J. B., & Kanwisher, N. (2016). Functional neuroanatomy of intuitive physical inference. *Proceedings of the national academy of sciences*, 113(34), E5072-E5081.
- Freud, E., Macdonald, S. N., Chen, J., Quinlan, D. J., Goodale, M. A., & Culham, J. C. (2018). Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. *Cortex*, 98, 34-48.
- Garcea, F. E., & Mahon, B. Z. (2014). Parcellation of left parietal tool representations by functional connectivity. *Neuropsychologia*, 60, 131-143.

- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton-Mifflin
- Goldenberg, G. (2017). Facets of pantomime. *Journal of the International Neuropsychological Society*, 23(2), 121-127.
- Hodges, J. R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia: Progressive fluent aphasia with temporal lobe atrophy. *Brain*, 115(6), 1783-1806.
- Ishibashi, R., Lambon Ralph, M. A., Saito, S., & Pobric, G. (2011). Different roles of lateral anterior temporal lobe and inferior parietal lobule in coding function and manipulation tool knowledge: evidence from an rTMS study. *Neuropsychologia*, 49(5), 1128-1135.
- Ishibashi, R., Mima, T., Fukuyama, H., & Pobric, G. (2018). Facilitation of function and manipulation knowledge of tools using transcranial direct current stimulation (tDCS). *Frontiers in integrative neuroscience*, 11, 37.
- Jax, S. A., & Buxbaum, L. J. (2010). Response interference between functional and structural actions linked to the same familiar object. *Cognition*, 115(2), 350-355.
- Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in neurosciences*, 18(7), 314-320.
- Jefferies, E., Thompson, H., Cornelissen, P., & Smallwood, J. (2020). The neurocognitive basis of knowledge about object identity and events: dissociations reflect opposing effects of semantic coherence and control. *Philosophical Transactions of the Royal Society B*, 375(1791), 20190300.
- Johnson-Frey, S. H. (2003). What's so special about human tool use?. *Neuron*, 39(2), 201-204.
- Kalénine, S., Peyrin, C., Pichat, C., Segebarth, C., Bonthoux, F., & Baciú, M. (2009). The sensory-motor specificity of taxonomic and thematic conceptual relations: A behavioral and fMRI study. *Neuroimage*, 44(3), 1152-1162.
- Kourtzi, Z., Betts, L. R., Sarkheil, P., & Welchman, A. E. (2005). Distributed neural plasticity for shape learning in the human visual cortex. *PLoS biology*, 3(7), e204.
- Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences*, 103(10), 3863-3868.
- Knights, E., Mansfield, C., Tonin, D., Saada, J., Smith, F. W., & Rossit, S. (2021). Hand-selective visual regions represent how to grasp 3D tools: brain decoding during real actions. *Journal of Neuroscience*, 41(24), 5263-5273.
- Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, 18(1), 42-55.

- Lesourd, M., Servant, M., Baumard, J., Reynaud, E., Ecochard, C., Medjaoui, F. T., ... & Osiurak, F. (2021). Semantic and action tool knowledge in the brain: identifying common and distinct networks. *Neuropsychologia*, 107918.
- Lewis, J. W. (2006). Cortical networks related to human use of tools. *The Neuroscientist*, 12(3), 211-231.
- Liuzzi, A. G., Aglinskias, A., & Fairhall, S. L. (2020). General and feature-based semantic representations in the semantic network. *Scientific Reports*, 10(1), 1-12.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of physiology-Paris*, 102(1-3), 59-70.
- Marstaller, L., Fynes-Clinton, S., Burianová, H., & Reutens, D. C. (2018). Evidence for a functional specialization of ventral anterior temporal lobe for language. *NeuroImage*, 183, 800-810.
- Martin, A. (2016). GRAPES—Grounding representations in action, perception, and emotion systems: How object properties and categories are represented in the human brain. *Psychonomic bulletin & review*, 23(4), 979-990.
- Milner, A. D., & Goodale, M. (2006). *The visual brain in action* (2nd Edition). Oxford University Press, Oxford
- Montagu, A. (1976). Toolmaking, hunting, and the origin of language. *Annals of the New York Academy of Sciences*, 280(1), 266-274.
- Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S., & Hodges, J. R. (2000). A voxel-based morphometry study of semantic dementia: relationship between temporal lobe atrophy and semantic memory. *Annals of neurology*, 47(1), 36-45.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological review*, 123(5), 534.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature reviews neuroscience*, 8(12), 976-987.
- Peelen, M. V., & Caramazza, A. (2012). Conceptual object representations in human anterior temporal cortex. *Journal of Neuroscience*, 32(45), 15728-15736.
- Prado, J., Clavagnier, S., Otzenberger, H., Scheiber, C., Kennedy, H., & Perenin, M. T. (2005). Two cortical systems for reaching in central and peripheral vision. *Neuron*, 48(5), 849-858.

- Putt, S. S., Wijekumar, S., Franciscus, R. G., & Spencer, J. P. (2017). The functional brain networks that underlie Early Stone Age tool manufacture. *Nature Human Behaviour*, 1(6), 1-8.
- Reynaud, E., Lesourd, M., Navarro, J., & Osiurak, F. (2016). On the neurocognitive origins of human tool use: A critical review of neuroimaging data. *Neuroscience & Biobehavioral Reviews*, 64, 421-437.
- Rossit, S., McAdam, T., Mclean, D. A., Goodale, M. A., & Culham, J. C. (2013). fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. *Cortex*, 49(9), 2525-2541.
- Rumiati, R. I., & Humphreys, G. W. (1998). Recognition by action: dissociating visual and semantic routes to action in normal observers. *Journal of Experimental Psychology: Human Perception and Performance*, 24(2), 631.
- Scholz, J., Klein, M. C., Behrens, T. E., & Johansen-Berg, H. (2009). Training induces changes in white-matter architecture. *Nature neuroscience*, 12(11), 1370-1371.
- Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., ... & Coslett, H. B. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences*, 108(20), 8520-8524.
- Schwettmann, S., Tenenbaum, J. B., & Kanwisher, N. (2019). Invariant representations of mass in the human brain. *Elife*, 8, e46619.
- Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential?. *Clinical neurophysiology*, 117(11), 2341-2356.
- Smith, F. W., & Goodale, M. A. (2015). Decoding visual object categories in early somatosensory cortex. *Cerebral cortex*, 25(4), 1020-1031.
- Snow, J. C., & Culham, J. C. (2021). The treachery of images: how realism influences brain and behavior. *Trends in Cognitive Sciences*.
- Snow, J. C., Pettypiece, C. E., McAdam, T. D., McLean, A. D., Stroman, P. W., Goodale, M. A., & Culham, J. C. (2011). Bringing the real world into the fMRI scanner: Repetition effects for pictures versus real objects. *Scientific reports*, 1(1), 1-10.
- Stout, D., & Chaminade, T. (2012). Stone tools, language and the brain in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 75-87.
- Styrkowiec, P. P., Nowik, A. M., & Króliczak, G. (2019). The neural underpinnings of haptically guided functional grasping of tools: an fMRI study. *Neuroimage*, 194, 149-162.

Tak, Y. W., Knights, E., Henson, R., & Zeidman, P. (2021). Ageing and the ipsilateral M1 BOLD response: a connectivity study. *Brain sciences*, 11(9), 1130.

Thibault, S., Py, R., Gervasi, A. M., Salemme, R., Koun, E., Lövdén, M., ... & Brozzoli, C. (2021). Tool use and language share syntactic processes and neural patterns in the basal ganglia. *Science*, 374(6569), eabe0874.

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human perception and performance*, 24(3), 830.

Valyear, K. (2016). The neuroscience of human tool use. In *Evolution of Nervous Systems: Second Edition* (pp. 341-353). Academic Press.

Valyear, K. F., Gallivan, J. P., McLean, D. A., & Culham, J. C. (2012). fMRI repetition suppression for familiar but not arbitrary actions with tools. *Journal of Neuroscience*, 32(12), 4247-4259.

Weisberg, J., Van Turenout, M., & Martin, A. (2006). A neural system for learning about object function. *Cerebral Cortex*, 17(3), 513-521.

Xia M, Wang J, He Y (2013) BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. *PLoS ONE* 8: e68910.

Young, G. (2006). Are different affordances subserved by different neural pathways?. *Brain and Cognition*, 62(2), 134-142.

Zagha, E., Erlich, J. C., Lee, S., Lur, G., O'Connor, D. H., Steinmetz, N. A., ... & Yang, H. (2022). The importance of accounting for movement when relating neuronal activity to sensory and cognitive processes. *Journal of Neuroscience*. <https://doi.org/10.1523/JNEUROSCI.1919-21.2021>

Declarations

Competing Interests:

The authors have no competing interests to disclose.

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Author contributions:

S.R., E.K. and F.W.S. conceptualised the study; E.K. and S.R. collected data; E.K., F.W.S and S.R. analysed data; E.K., F.W.S. and S.R. wrote the manuscript; S.R. and F.W.S. acquired funding.

Figures

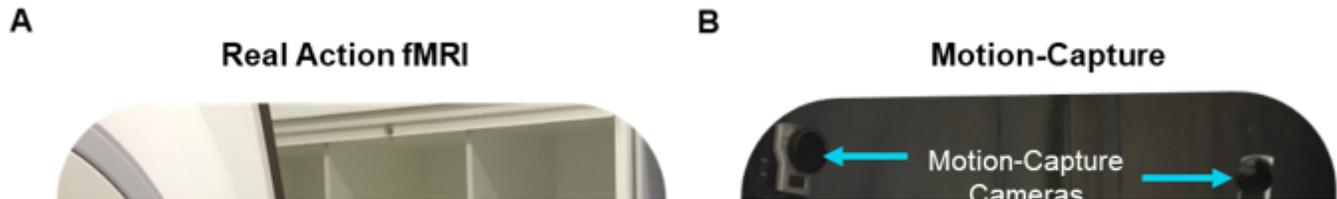


Figure 1

(A) fMRI Experiment. Participants laid under a custom-built MR-compatible turntable where 3D-printed tool and non-tool stimuli were presented within reaching distance in a block-design. **(B) Motion-Capture Experiment.** As a behavioural control experiment, participants performed this paradigm in a motion-capture laboratory to measure kinematics with infrared-reflective (IRED) markers affixed to the hand. **(A & B).** During the experiments, the rooms were completely dark, objects were visible only when illuminated, all actions were performed with the right-hand only and participants were naïve to study goals (i.e., they were asked to grasp right or left side of objects without mentioning we were investigating tools or typicality manipulation).

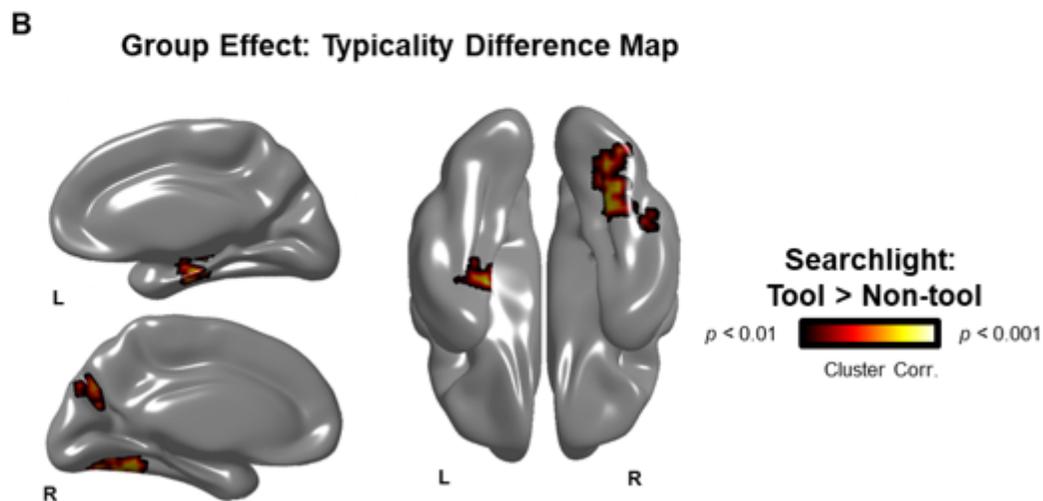
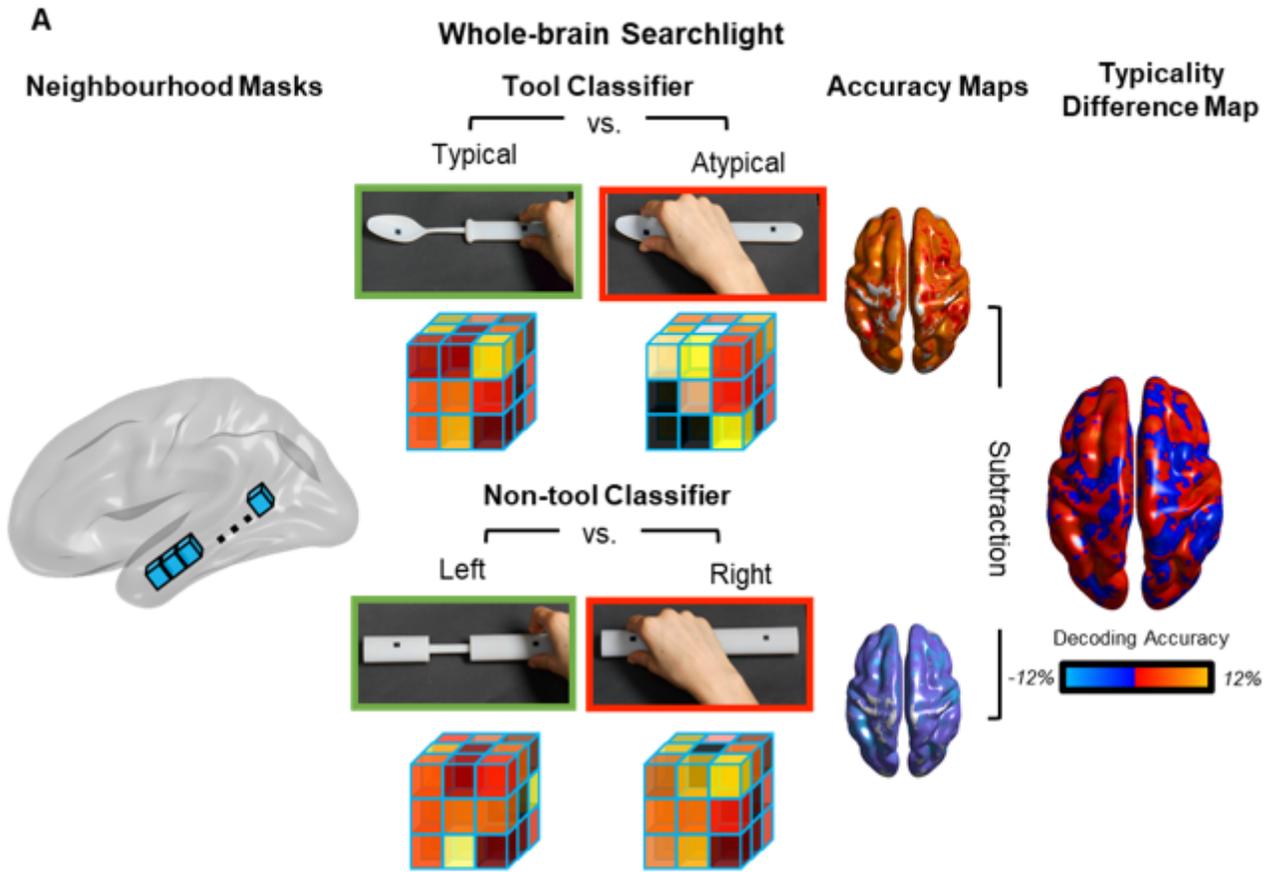


Figure 2

(A) Wholebrain searchlight classification. For each participant, brain activation patterns were extracted from a mask (single blue cube) that was shifted through the entire fMRI volume. Decoding accuracy was measured with independent linear pattern classifiers for tool (top row) and non-tool actions (bottom row) that were trained to map between brain-activity patterns and the type of grasp being performed with the tools (typical vs atypical) or non-tools (right vs left). Typicality difference maps were produced by subtracting the decoding accuracy maps for tools and non-tools, as well as chance-level accuracy (50%).

(B) Searchlight Results. The group typicality difference map demonstrated clusters in the left anterior

temporal cortex, as well as right medial parietal and fusiform areas, where decoding accuracies were significantly higher for actions with tools (typical vs. atypical grasps) than non-tools (biomechanically equivalent right vs. left grasps).

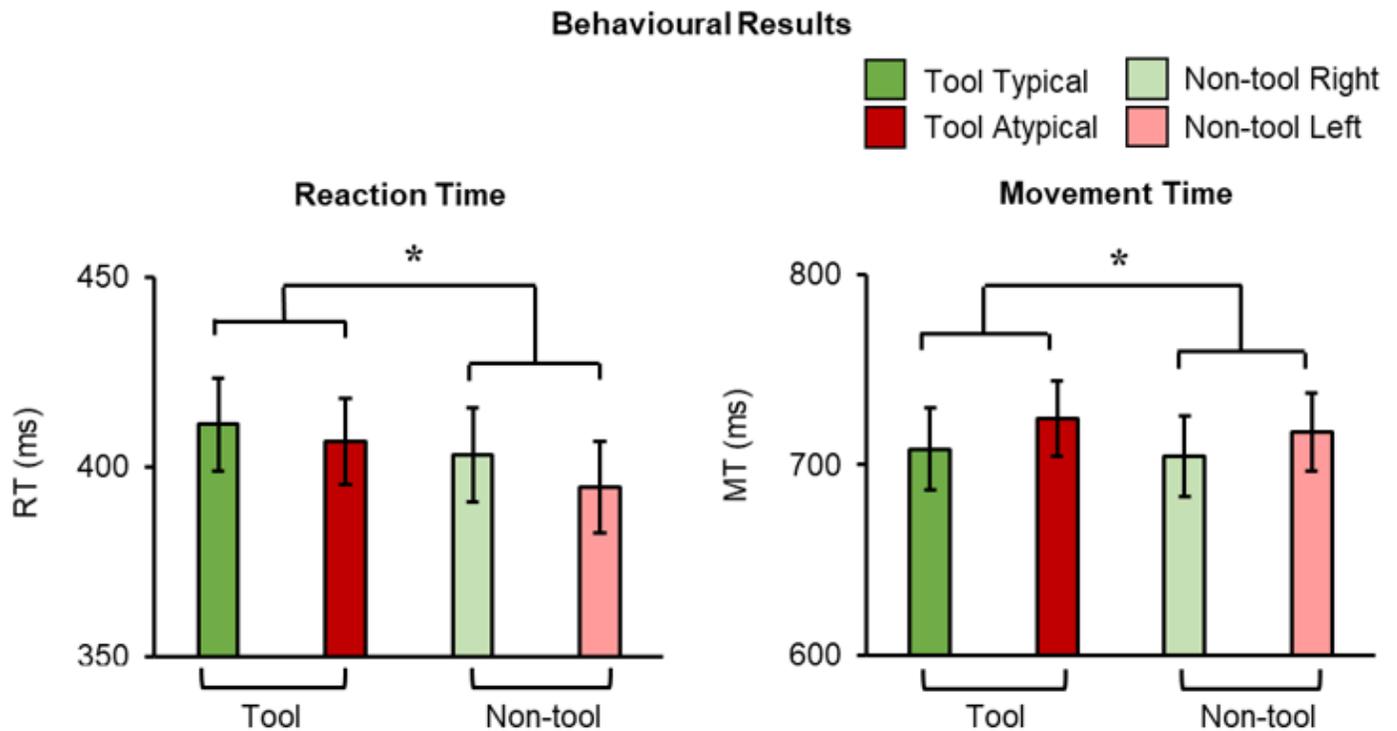


Figure 3

Behavioural Results. Hand kinematics differed between object categories: participant's RTs and MTs were slower when grasping tools, relative to non-tools. Error bars represent standard error of the mean.

Supplementary Files

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