Check for updates

Independent Representations of Verbs and Actions in Left Lateral Temporal Cortex

Marius V. Peelen[1,2], Domenica Romagno[3], and Alfonso Caramazza[1,2]

Abstract

■ Verbs and nouns differ not only on formal linguistic grounds but also in what they typically refer to: Verbs typically refer to actions, whereas nouns typically refer to objects. Prior neuroimaging studies have revealed that regions in the left lateral temporal cortex (LTC), including the left posterior middle temporal gyrus (pMTG), respond selectively to action verbs relative to object nouns. Other studies have implicated the left pMTG in action knowledge, raising the possibility that verb selectivity in LTC may primarily reflect action-specific semantic features. Here, using functional neuroimaging, we test this hypothesis. Participants performed a simple memory task on visually presented verbs and nouns that described either events (e.g., "he eats" and "the conversation") or states (e.g., "he exists" and "the value"). Verb-selective regions in the left pMTG and the left STS were defined in individual participants by an independent localizer contrast between action verbs and object nouns. Both regions showed equally strong selectivity for event and state verbs relative to semantically matched nouns. The left STS responded more to states than events, whereas there was no difference between states and events in the left pMTG. Finally, whole-brain group analysis revealed that action verbs, relative to state verbs, activated a cluster in pMTG that was located posterior to the verb-selective pMTG clusters. Together, these results indicate that verb selectivity in LTC is independent of action representations. We consider other differences between verbs and nouns that may underlie verb selectivity in LTC, including the verb property of predication. ■

INTRODUCTION

Nouns and verbs are elemental grammatical units of most, if not all, human languages. Nouns and verbs are identified on the basis of formal morphosyntactic features. For example, nouns bear nominal markers, and verbs bear verbal markers. Moreover, verbs and nouns are associated with distinct syntactic patterns and play different roles in sentences. The categories of verb and noun are, therefore, formally discrete, in so far as they are encoded by clear-cut linguistic units.

However, nouns and verbs differ not only on formal linguistic grounds but also differ in what they typically refer to. Nouns typically (but not always) refer to entities, whereas verbs typically (but not always) refer to events. It is possible to identify prototypical members of each category. Prototypical verbs denote agentive dynamic actions, such as *to walk* and *to build*; prototypical nouns denote concrete three-dimensional individualized entities, such as *the table* and *the professor*. But verbs may also refer to states (*to stay*) or relations (*to belong*), and nouns may also refer to events (*the wedding*) or conditions (*the temperature*; Hopper & Thompson, 1984; Lyons, 1977).

Prior functional neuroimaging studies have revealed brain regions selectively engaged in verb processing (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012; Willms et al., 2011; Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Shapiro, Moo, & Caramazza, 2006; Yokoyama et al., 2006; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Perani et al., 1999), although there appears to be considerable variability across studies in the specific regions reported (Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011), which is presumably related to differences in tasks and/or stimuli. The most consistent finding across studies is a selective involvement of the left lateral temporal cortex (LTC), including the posterior middle temporal gyrus (pMTG), in verb processing (Bedny et al., 2008, 2012; Crepaldi et al., 2011; Willms et al., 2011; Burton, Krebs-Noble, Gullapalli, & Berndt, 2009; Tyler, Randall, & Stamatakis, 2008; Shapiro et al., 2006; Perani et al., 1999). Because these prior studies have generally contrasted action verbs with object nouns, it is unknown whether verb-selective responses in LTC reflect lexical, syntactic, and/or semantic differences between verbs and nouns.

Interestingly, the left LTC has also been consistently implicated in conceptual action and tool knowledge (Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Campanella, D'Agostini, Skrap, & Shallice, 2010; Kalenine, Buxbaum, & Coslett, 2010; Martin, 2007; Kable et al., 2005; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003; Chao, Haxby, & Martin, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). This raises the possibility that verb selectivity in the left LTC may be driven primarily by semantic differences between action verbs and object nouns. Indeed, several studies have found that sentences referring to actions activate regions in LTC (Wallentin et al., 2011;

[1]University of Trento, [2]Harvard University, [3]University of Pisa

© 2012 Massachusetts Institute of Technology

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1778449/jocn_a_00257.pdf by guest on 17 May 2021

Deen & McCarthy, 2010; Rueschemeyer, Glenberg, Kaschak, Mueller, & Friederici, 2010; Saygin, McCullough, Alac, & Emmorey, 2010; Hauk, Davis, Kherif, & Pulvermuller, 2008; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005; Davis, Meunier, & Marslen-Wilson, 2004), including a verb-selective region in STS (Davis et al., 2004). However, a recent study investigating responses in functionally localized verb-selective LTC regions showed that these regions are not modulated by the amount of visual motion or motor activity associated with verbs, with equally selective responses to verbs such as *to jump* and *to think* (Bedny et al., 2008). Furthermore, verb-selective LTC responses have also been reported in congenitally blind participants (Bedny et al., 2012), excluding the possibility that selectivity for action verbs in LTC relates to visual motion.

Importantly, however, actions also differ from objects at a more abstract conceptual level, such as the understanding of actions (but not objects) as dynamic events unfolding over time. Thus, rather than or in addition to representing basic sensory motor features, verb-selective LTC may very well represent these more abstract semantic differences between actions (including mental actions) and objects. In this study, we tested this hypothesis by disentangling grammatical category from prototypical semantic features of verbs and nouns.

If verb selectivity in LTC reflects the retrieval of event concepts, we would expect (1) that activity in LTC would be relatively low to verbs that do not refer to events (e.g., *to include*) relative to verbs that do (e.g., *to talk*) and (2) that activity in LTC would be relatively high to nouns that refer to events (e.g., *the run*) relative to nouns that do not (e.g., *the identity*). To test these predictions, we performed two experiments in which grammatical category (verb, noun) and dynamicity (state, event) were manipulated in a 2 × 2 factorial design. Both experiments also included separate action verb and object noun conditions to localize LTC regions reported in previous studies (Bedny et al., 2008, 2012; Willms et al., 2011; Burton et al., 2009; Tyler et al., 2008; Shapiro et al., 2006; Perani et al., 1999). To ensure that results were not specific to a particular stimulus set, the two otherwise identical experiments differed in the stimulus material used: in Experiment 1, all the noun phrases had a shared root with a verb (e.g., *the desire*), whereas in Experiment 2 none of the noun phrases had a shared root with a verb. Furthermore, in Experiment 1 all verb phrases had an animate subject ("he" or "she"), whereas in Experiment 2 all verb phrases had an inanimate subject ("this").

METHODS

Participants

A total of 27 healthy adult volunteers (12 women; mean age = 26 years, age range = 20–36 years) participated in the study (Experiment 1: n = 15; Experiment 2: n = 12). All participants were native Italian speakers and right-handed and had normal or corrected-to-normal vision and no history of neurological or psychiatric disease. Participants gave written informed consent for participation in the study, which was approved by the human research ethics committee of the University of Trento.

Two participants (one in each experiment) were excluded due to excessive head motion (>4 mm in any direction across the experiment). One participant (from Experiment 1) was excluded due to low performance (mean accuracy of <3 standard deviations of the group mean). This left a total of 13 participants in Experiment 1 and 11 participants in Experiment 2.

Stimuli

For both experiments, stimuli consisted of 20 short phrases per condition (in Italian), such as "she talks" and "the temperature" (Appendix). There were four experimental conditions: event verbs (EV; e.g., "this arrives"), event nouns (EN; e.g., "the conference"), state verbs (SV; e.g., "this contains"), and state nouns (SN; e.g., "the identity"). Two additional conditions were included to localize regions previously implicated in verb processing: action verbs (AV; e.g., "he jumps") and object nouns (ON; e.g., "the lamp"). We use the label "action verbs" (rather than "event verbs") for the localizer condition because all phrases denoted motor actions. It should be noted, however, that there is considerable semantic overlap between the action verb and event verb conditions: all action verbs describe events, and many event verbs describe motor actions (see Appendix). The action verb and object noun conditions were included for the purpose of having a statistically independent localizer for verb selective ROIs, one that used stimuli similar to those used in many previous studies.

Event verbs denoted dynamic activities unfolding over time, such as "he chases" and "this arrives," whereas state verbs denoted states or conditions represented above time, such as "he exists" and "this includes." Event and state nouns paralleled verb semantics, as they denote dynamic events, like "the destruction" and "the excursion," or states and conditions, like "the existence" and "the temperature." The phrases of the four experimental conditions were matched for cumulative and form frequency (Bertinetto et al., 2005), word length in letters, and grammatical gender of nouns and pronouns that preceded verbs. We included both one-argument verbs, such as *to walk*, and two-argument verbs, such as *to build*. The number of arguments of the verbs was matched across conditions.

Different phrases were used in the two experiments (Appendix). The AV and ON conditions used to localize ROIs were identical for the two experiments. For Experiment 1, EV and SV phrases had an animate subject ("he" or "she"), whereas in Experiment 2, EV and SV phrases had an inanimate subject ("this"). In Experiment 1, all

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1945759/jocn_a_00257.pdf by guest on 17 May 2021

the EN and SN phrases had a shared root with a verb (e.g., "the desire"), whereas in Experiment 2 none of the EN and SN phrases had a shared root with a verb.

To account for differences in imageability, age of acquisition, and familiarity, all phrases were rated on these variables on a 1–7 scale (Bates, Burani, D'Amico, & Barca, 2001) by two groups of healthy native Italian volunteers ($n = 24$ for the phrases used in Experiment 1; $n = 42$ for the phrases used in Experiment 2). The rating instructions and scales were identical to those used in Bates et al. (2001). Mean ratings for each condition can be found in the Appendix. Ratings were included as regressors of no interest in the fMRI analysis (see Data analysis).

Task and Design

The design of the two experiments was identical. Participants performed six runs of the fMRI experiment, each consisting of 24 blocks. Each block consisted of four short phrases of one of the six conditions (EV, EN, SV, SN, AV, ON), with each condition occurring four times in a run, in random order. The fourth phrase of each block was presented in green instead of white. The task of the participants was to decide whether this probe phrase was identical to one of the three preceding phrases, which was true on 50% of the blocks. They pressed a button with their index finger to answer "yes" and another button with their middle finger to answer "no." Within a block, the first three phrases were presented for 1.5 sec, each followed by a 0.5-sec interval, for a total of 6 sec. Between the third phrase and the probe phrase, an extra 1.5-sec interval was added. The probe phrase was presented for 1 sec, followed by an intertrial interval of 2.5 sec, during which participants made their response. The total block duration was thus 11.0 sec. Each run started and ended with a 13-sec fixation period.

The first three (nonidentical) phrases of each block were randomly drawn from the total set of 20 phrases per condition. For target blocks, the probe phrase was randomly selected from one of the three preceding phrases. For nontarget blocks, the probe phrase was randomly selected from the remaining set of 17 phrases. Because the total number of trials (576) exceeded the total number of available phrases (120), each phrase was repeated several times over the course of the experiment, which could have resulted in an overall weaker BOLD signal than if all phrases were unique.

Data Acquisition

Functional and structural data were collected at the Center for Mind/Brain Sciences, University of Trento, Italy. All images were acquired on a Bruker BioSpin MedSpec 4-T scanner (Bruker BioSpin GmbH, Rheinstetten, Germany). Functional images were acquired using EPI T2*-weighted scans. Acquisition parameters were repetition time of 2 sec, an echo time of 33 msec, a flip angle of 73°, a field of view of 192 mm, and a matrix size of 64×64. Each functional acquisition consisted of 34 axial slices (which covered the whole cerebral cortex) with a thickness of 3 mm and gap of 33% (1 mm). Structural images were acquired with an MPRAGE sequence with $1 \times 1 \times 1$ mm resolution.

Data Analysis

Data were analyzed using the AFNI software package (afni.nimh.nih.gov/) and MATLAB (The MathWorks, Natick, MA). Functional data were slice-time corrected, motion corrected, and low-frequency drifts were removed with a temporal high-pass filter (cutoff of 0.006 Hz). Data were spatially smoothed with a Gaussian kernel (6 mm FWHM).

For each participant, general linear models were created to model the six conditions of the experiment. Statistical maps were transformed into Talairach space and resampled to $3 \times 3 \times 3$ mm. Events consisted of the first 8.5 sec of each block, which included the presentation of the four phrases but excluded the intertrial interval during which responses were made. These events were convolved with a standard model of the hemodynamic response function. Regressors of no interest were also included to account for differences in the mean MR signal across scans and for head motion within scans. Three additional regressors were included to account for differences in imageability, age of acquisition, and familiarity. For each of these three variables, the ratings (on a 1–7 scale) of the total set of 120 phrases were first z-normalized by subtracting the mean rating from the individual ratings and dividing the difference by the standard deviation of the mean. Next, for each individual phrase presented in the experiment, the normalized ratings were convolved (multiplied) with a standard model of the hemodynamic response function.

Whole-brain random-effects group analyses were performed on the data of both experiments combined. The statistical threshold was determined using AFNI's AlphaSim, which performs alpha probability simulations taking into account the smoothness of the data. At a threshold of $p < .0001$ the probability that a random field of noise would produce a cluster of 11 or more (resampled) voxels (>297 mm^3) was less than 5% ($p < .05$). This threshold was adopted unless otherwise specified.

Definition of ROIs

ROIs were defined in individual participants and were restricted to voxels that were significantly activated in the corresponding group analysis (the results of the group analyses are given in Table 1). The same contrast that was used in the group analysis (AV > ON) was also used in each individual participant, applying an individual participant voxel threshold of $p < .05$ (uncorrected). No cluster size threshold was applied at the individual participant level. The first ROI, pMTG, defined by the contrast AV > ON, could be localized in all 24 participants and had

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2095/1945715/jocn_a_00257.pdf by guest on 17 May 2021

Table 1. Overview of Activated Regions in Whole-brain Random-effects Group Analyses ($n = 24$), Thresholded at $p < .05$ (Corrected for Multiple Comparisons)

Contrast	*Region*	*Coordinates* *x*	*y*	*z*	*Volume (mm³)*
AV > ON	Left MTG/STS	−51	−30	4	567
	Left pMTG	−49	−53	12	1917
	Left TPJ	−57	−46	24	324
	Right IOG	32	−80	−5	1944
ON > AV	Left FG	−26	−33	−17	864
SV > SN	Left MTG/STS	−61	−25	3	405

Coordinates are of the center of mass of the clusters, in Talairach space. IOG, inferior occipital gyrus; FG, fusiform gyrus.

a mean size of 893 mm^3. The second ROI, MTG/STS, defined by the contrast AV > ON, could be localized in 19 participants (9 of Experiment 1, 10 of Experiment 2), and had a mean size of 347 mm^3.

RESULTS

Behavioral Results

Mean accuracy did not differ between AV and ON conditions (AV: 96.5%; ON: 96.9%; $t(23) = -0.3$, $p = .74$). Mean RT did not significantly differ either (AV: 834 msec; ON: 819 msec; $t(23) = 1.1$, $p = .29$).

Accuracy and RT of the experimental conditions (EV, EN, SV, SN) were analyzed in 2 × 2 ANOVAs with Dynamicity (event, state), and Grammatical Class (verb, noun) as factors. There was a main effect of Grammatical Class, $F(1, 22) = 5.3$, $p = .032$, with (slightly) higher accuracy for nouns (97.8%) than verbs (96.4%). There was no significant effect of Dynamicity, $F(1, 22) = 2.7$, $p = .11$, indicating equally high accuracy for events (96.5%) and states (97.7%). The interaction between Grammatical Class and Dynamicity was not significant ($p = .12$). For RT, there was a main effect of Grammatical Class ($F(1, 22) = 5.1$, $p = .034$), with faster responses to nouns (813 msec) than to verbs (831 msec). There was again no significant effect of Dynamicity, $F(1, 22) = 0.6$, $p = .45$, indicating equally fast responses to events (819 msec) and states (825 msec). The interaction between Grammatical Class and Dynamicity was not significant ($p = .78$).

Results of Whole-brain Group Analyses

The first analysis was aimed at replicating and localizing verb-selective responses in LTC. Following earlier work (Bedny et al., 2008, 2012; Willms et al., 2011; Tyler et al., 2008; Shapiro et al., 2006), we contrasted activity in response to action verbs (e.g., "he jumps") with activity to object nouns (e.g., "the lamp") in a whole-brain random-effects group analysis. As expected, significant activity was observed in the left LTC (Table 1). The activity in LTC consisted of a cluster in the pMTG and a more anterior cluster in the MTG/STS. Verb-selective activity was also observed in the left TPJ and the right inferior occipital gyrus. A region in the left medial fusiform gyrus responded more to object nouns than to action verbs (Table 1).

To test whether verb-selective regions could also be observed for verbs that do not refer to actions or events, we contrasted state verbs with state nouns. This contrast again yielded significant activity in left LTC (Table 1). No regions showed more activity to nouns than verbs in this analysis.

What is the relation between action and verb representations in LTC? To address this question, we compared LTC activity to three different contrasts at more lenient statistical thresholds ($p < .005$, uncorrected), limiting the analysis to the LTC. The first contrast was between action verbs and object nouns, a contrast expected to activate both action and verb representations. The second contrast, between state verbs and state nouns, probes verb but not action representations. The third contrast, between action verbs and state verbs, probes action but not verb representations. The results are displayed in Figure 1. Interestingly, an action-selective cluster (Figure 1; AV > SV) was found posterior to verb-selective clusters (Figure 1; SV > SN), indicating that nearby but distinct clusters may represent verbs and actions. At this relatively lenient threshold, the contrast between action verbs and object nouns activated both verb- and action-selective cluster (Figure 1; AV > ON). At more stringent thresholds (Table 1), the AV > ON contrast primarily activated verb-selective regions.

Finally, we tested for differences between responses to events and states, averaged across grammatical category. No regions responded differentially to these categories at

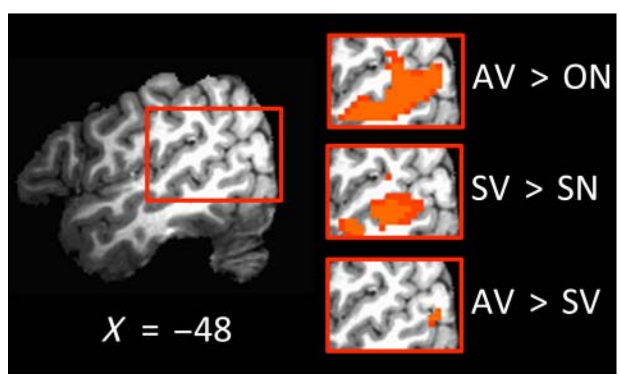

Figure 1. Verb- and action-selective clusters in the left LTC. Results of three independent contrasts are shown at $p < .005$ (uncorrected): action verbs versus object nouns (AV > ON; top row), state verbs versus state nouns (SV > SN; middle row), and action verbs versus state verbs (AV > SV; bottom row). These results reveal two verb-selective LTC clusters, in pMTG and MTG/STS, for nonaction verbs (SV > SN) and also indicate that distinct regions encode verbs (SV > SN) and actions (AV > SV).

Downloaded from http:// ... user on 17 May 2021

the corrected statistical threshold. At a more lenient threshold ($p < .005$, uncorrected), activity was observed in the left LTC ($xyz = -47, -30, -2$), with stronger responses to states than events.

Results of ROI Analysis

To test whether verb-selective responses in left LTC reflect the retrieval of event concepts, we compared responses to the four experimental conditions (EV, EN, SV, SN) within LTC ROIs defined by the independent contrast between AV and ON. In the whole-brain group analysis (at $p < .05$, corrected), this contrast revealed activity in two separate regions of LTC (pMTG and MTG/STS; Table 1; note that these regions merged at the more lenient threshold displayed in Figure 1). Responses in both these regions were further investigated by localizing them in individual participants (see Methods). Responses were analyzed for each ROI separately using mixed $2 \times 2 \times 2$ ANOVAs with Experiment (1, 2), Dynamicity (event, state), and Grammatical Class (verb, noun) as factors.

pMTG, localized in individual participants, showed a main effect of Grammatical Class, $F(1, 22) = 29.3$, $p = .00002$, with stronger responses to verbs than nouns (Figure 2). This result indicates that verb selectivity in pMTG generalizes to semantically matched verb–noun contrasts. The interaction between Grammatical Class and Experiment approached significance, $F(1, 22) = 4.2$, $p = .054$, with a stronger difference between verbs and nouns in Experiment 2, $t(10) = 6.6$, $p = .00006$, than in Experiment 1, $t(12) = 2.2$, $p = .052$. There were no significant effects involving the factor Dynamicity (main effect: $F(1, 22) = 0.0$, $p = .95$; Dynamicity × Grammatical Class: $F(1, 22) = 2.7$, $p = .12$; Dynamicity × Experiment: $F(1, 22) = 1.3$, $p = .28$; Dynamicity × Experiment × Grammatical Class: $F(1, 22) = 0.0$, $p = .91$).

A similar pattern of results was obtained when pMTG was localized based on group-average activity without individual participant voxel selection: a main effect of Grammatical Class ($F(1, 22) = 19.5$, $p = .0002$), an interaction between Grammatical Class and Experiment ($F(1, 22) = 5.9$, $p = .024$), and again no significant effects involving the factor Dynamicity ($p > .18$, for all tests).

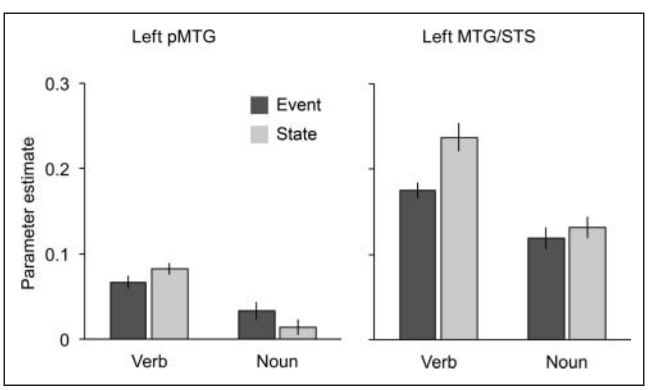

Figure 2. Responses to the four experimental conditions in left LTC ROIs (pMTG and MTG/STS), defined by the contrast AV > ON. Error bars indicate within-subject *SEM*.

The MTG/STS ROI, defined by the contrast AV > ON in individual participants, showed a main effect of Grammatical Class, $F(1, 17) = 25.6$, $p = .0001$, with stronger responses to verbs than nouns (Figure 2). The interaction between Grammatical Class and Experiment was significant, $F(1, 17) = 5.9$, $p = .027$, with a stronger difference between verbs and nouns in Experiment 2, $t(9) = 4.7$, $p = .001$, than in Experiment 1, $t(8) = 2.3$, $p = .052$. There was a significant main effect of Dynamicity, $F(1, 17) = 8.5$, $p = .010$, with stronger responses to states than events (Figure 2). There were no significant interactions between Dynamicity and the other factors (Dynamicity × Grammatical Class: $F(1, 17) = 2.8$, $p = .11$; Dynamicity × Experiment: $F(1, 17) = 2.3$, $p = .14$; Dynamicity × Experiment × Grammatical Class: $F(1, 17) = 0.0$, $p = .97$).

A similar pattern of results was obtained when MTG/STS was localized based on group-average activity without individual participant voxel selection: a main effect of Grammatical Class, $F(1, 22) = 16.2$, $p = .0006$; an interaction between Grammatical Class and Experiment, $F(1, 22) = 4.8$, $p = .039$; and again a significant main effect of Dynamicity, $F(1, 22) = 5.0$, $p = .035$, with stronger responses to states than events.

Finally, we tested whether verb-selective regions in LTC distinguished between the three verb types (action, event, state) and/or between the three noun types (object, event, state). Because the ROIs used in the previous analyses were defined by the localizer contrast between action verbs and object nouns, comparing verb/noun types within these ROIs would be statistically biased toward action verbs and against object nouns. Therefore, we defined verb-selective regions (pMTG and MTG/STS) using the contrast between all verbs and all nouns based on group average activity. Within these regions, we then tested for differences between the verb and noun types in 2×3 ANOVAs, with Experiment (1, 2) and Verb or Noun type (events, states, actions/objects) as factors.

pMTG showed no main effect of Verb type, $F(2, 21) = 2.4$, $p = .11$, and no interaction between Verb type and Experiment, $F(2, 21) = 0.8$, $p = .45$. MTG/STS showed a main effect of Verb type, $F(2, 21) = 4.3$, $p = .028$, but no interaction between Verb type and Experiment, $F(2, 21) = 1.6$, $p = .22$. The main effect of Verb type was driven by a stronger response to state verbs than to event verbs, $t(23) = 2.9$, $p = .009$, confirming the results of the analyses in MTG/STS defined by AV > ON. There were no significant differences between action and event verbs, $t(23) = 1.7$, $p = .11$, or between state and action verbs, $t(23) = 1.3$, $p = .20$.

pMTG showed a main effect of Noun type, $F(2, 21) = 5.7$, $p = .011$, but no interaction between Noun type and Experiment, $F(2, 21) = 1.1$, $p = .34$. The main effect of Noun type was driven by a lower response to object nouns relative to both state and event nouns, $t(23) > 2.3$, $p < .05$, for both tests. There was no significant difference between

Downloaded from http://... user on 17 May 2021

state and event nouns, $t(23) = 1.4, p = .18$. The main effect of Noun type in MTG/STS did not reach significance, $F(2, 21) = 2.9, p = .078$, and there was no interaction between Noun type and Experiment, $F(2, 21) = 1.7, p = .20$. Pairwise t tests showed a stronger response to state nouns than object nouns, $t(23) = 2.2, p = .039$, but no difference between state nouns and event nouns, $t(23) = 0.7, p = .52$, or between event nouns and object nouns, $t(23) = 1.3, p = .20$.

DISCUSSION

This study tested whether and how neural selectivity for verbs in the left LTC is related to the representation of conceptual action knowledge. We first replicated previous studies by contrasting action verbs with object nouns. This contrast gave significant verb-selective activity in a region in the left MTG/STS and a more posterior region in the left pMTG that was present in all 24 participants. Verb-selective activity in LTC was also observed for the contrast between nonaction (state) verbs and state nouns, with activity in both pMTG and MTG/STS at more lenient statistical thresholds (Figure 1). Activity selective for action verbs, relative to state verbs, was found posterior to verb-selective clusters. We then tested for differences between verbs and nouns that referred to states and events within functionally defined ROIs. Verb-selective LTC regions, defined by their preference for action verbs over object nouns, also responded selectively to state and event verbs when contrasted with state and event nouns (e.g., "he runs" vs. "the run"). Furthermore, neither MTG/STS nor pMTG responded more to events than states. Instead, in the MTG/STS region, the opposite result was found, with stronger responses to states than events. Together, these results show that selectivity for action verbs in LTC cannot be fully accounted for by semantic differences between actions as agentive dynamic events and objects as concrete three-dimensional entities.

Although verb selectivity in LTC may not directly reflect the retrieval of action concepts, as shown in this study, it is probably no coincidence that both verbs and conceptual action knowledge recruit the left posterior MTG (Kemmerer et al., 2012; Campanella et al., 2010; Kalenine et al., 2010; Martin, 2007; Tranel et al., 2003; Martin et al., 1995). Considering the fact that most verbs describe actions, it would be efficient for the brain to represent verbs close to regions representing action knowledge, as shown here (Figure 1). Importantly though, the present data suggest that verb processing and action knowledge, although represented nearby, are distinct processes.

What could be the critical difference between verbs and nouns that drives activity in the left LTC? One possibility is that this region is involved in morphosyntactic processing needed for the correct inflectional form of verbs (Tyler et al., 2008; Tyler, Bright, Fletcher, & Stamatakis, 2004). Although we cannot exclude this possibility, it seems unlikely given that verb inflection was irrelevant to the present memory task. Further evidence against this possibility is provided by experiments involving semantic judgments of uninflected verbs and nouns that have found a verb effect in left LTC (Bedny et al., 2008, 2012). Alternatively or additionally, LTC may be involved in the verb property of linking arguments within a sentence (Shetreet, Friedmann, & Hadar, 2010; den Ouden, Fix, Parrish, & Thompson, 2009; Thompson et al., 2007; Wu, Waller, & Chatterjee, 2007): Verbs specify that an agent does something ("he jumps"), has a certain property ("he stinks"), or does something with something else ("he builds houses"). Prototypical nouns lack this kind of predicative property (Lyons, 1977).

A surprising finding was the increased activation to states relative to events in the left MTG/STS, considering that nearby regions (though typically in the right hemisphere) have been implicated in the processing of biological motion (Peelen, Wiggett, & Downing, 2006; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; Allison, Puce, & McCarthy, 2000; Grossman et al., 2000). This difference was particularly pronounced for verbs (Figure 2), with higher activation for state verbs like "he exists" than event verbs like "he chases." Interestingly, a somewhat related preference for low-motion mental action verbs (e.g., *to think*) relative to high-motion action verbs (e.g., *to kick*) was observed in previous work (Bedny et al., 2008, 2012; Grossman et al., 2002). What could underlie this difference? One possibility is that the greater response for state verbs as compared with event verbs is related to the atypical semantic role of the subject: The subject of a state verb has the semantic role of undergoer, whereas typical subjects are agents (Van Valin & LaPolla, 1997; Givón, 1984). Another possibility may be that verbs that are distant from prototypical verbs (i.e., those that are less like agentive dynamic actions) recruit LTC more strongly.

Reduced verb selectivity in LTC was found for the stimuli used in Experiment 1 as compared with those used in Experiment 2. One difference between the experiments was the use of animate subjects in Experiment 1 ("he" or "she") and inanimate subjects ("this") in Experiment 2. Given the significant verb selectivity observed for the localizer conditions (action verbs vs. object nouns), which consistently used animate subjects, the relatively weak verb selectivity in Experiment 1 is unlikely to be related to the use of animate subjects. Perhaps more importantly, the nouns in Experiment 1 always had a verbal root, whereas those in Experiment 2 did not. Thus, nouns with verbal roots may partly activate verb-selective regions in LTC. Future studies should investigate this possibility more systematically.

In contrast to several previous studies (e.g., Willms et al., 2011; Palti, Ben Shachar, Hendler, & Hadar, 2007; Shapiro et al., 2006), we did not observe significant verb-selective activation in left pFC at the corrected statistical threshold, although our sample size ($N = 24$) was larger than most of these previous studies that similarly contrasted action verbs with object nouns. This difference may relate to our task, which consisted of the simple memorizing of phrases and did not require task-relevant processing of morphological features as in some previous studies (Willms et al., 2011;

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1945792/jocn_a_00257.pdf by guest on 17 May 2021

Palti et al., 2007; Shapiro et al., 2006). Indeed, two previous studies in which the task (a semantic relatedness task) similarly did not require morphosyntactic processing, verb-selective activity was found in the left pFC in only one of the studies (Bedny et al., 2008) whereas it was found in the left LTC in both studies (Bedny et al., 2008, 2012).

In summary, this study showed that verb selectivity in LTC is not restricted to action verbs but is similarly present for nonaction (state) verbs contrasted with semantically matched nouns. In addition, the absence of a positive difference between events and states suggests that verb selectivity in LTC is not related to the retrieval of event concepts. Although these results do not explain the critical component driving verb selectivity in LTC, they significantly reduce the range of possibilities by excluding an explanation solely related to the retrieval of conceptual action knowledge. Equally important, given that the verb-selective effect in LTC cuts across semantic verb categories, it implies a general grammatical class effect that is not reducible to specific semantic properties (such as action or event features). This leaves two possible organizational principles. One possibility is that the lexical distinction captured in LTC is a formal morphosyntactic property: a bundle of formal features that jointly serve to distinguish between nouns and verbs as morphosyntactically determined categories. The other possibility is that the distinction captured in LTC is that between words that typically do (verbs) and words that typically do not (nouns) have a predicative function. Predicates/verbs specify the types of roles or relations that arguments/nouns may take in a given situation, and as such can be thought of as a semantic rather than a syntactic category. This would be in line with results showing that LTC is implicated in conceptual processing. However, although we suspect that the latter possibility best captures the verb-selective activation in LTC, we still lack direct evidence for this claim, and we must await further theoretical analysis and experimental investigation before we can decide this issue conclusively.

APPENDIX

All the phrases used in the two experiments, with English translation. Also provided are the mean ratings for age of acquisition (higher ratings indicate older age of acquisition), familiarity (higher ratings indicate higher familiarity), and imageability (higher ratings indicate higher imageability), separately for each condition. Standard deviation across participants is provided in brackets.

Appendix.

	Experiment 1	*Experiment 2*
State verbs	Egli merita [he deserves]	Ciò include [this includes]
	Lei preferisce [she prefers]	Ciò implica [this implies]
	Lei dissente [she disagrees]	Ciò costa [this costs]
	Egli crede [he believes]	Ciò riguarda [this concerns]
	Lei presuppone [she presumes]	Ciò significa [this means]
	Lei eccelle [she excels]	Ciò caratterizza [this characterizes]
	Egli vale [he is worth]	Ciò contiene [this contains]
	Lei piace [she is liked]	Ciò vale [this is worth]
	Egli risiede [he resides]	Ciò dista [this is far from]
	Lei esiste [she exists]	Ciò depende [this depends]
	Lei eguaglia [she equates]	Ciò piace [this is liked]
	Egli puzza [he stinks]	Ciò esiste [this exists]
	Egli conosce [he knows]	Ciò manca [this lacks]
	Egli teme [he fears]	Ciò puzza [this stinks]
	Lei manca [she lacks]	Ciò abbonda [this abounds]
	Egli resta [he stays]	Ciò dispiace [this is not pleasant]
	Lei desidera [she desires]	Ciò sussiste [this subsists]
	Egli giace [he lies (down)]	Ciò comporta [this entails]
	Egli possiede [he owns]	Ciò incombe [this is incumbent]
	Lei sa [she knows]	Ciò appartiene [this belongs]

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2095/1777959/jocn_a_00257.pdf by guest on ... user on 17 May 2021

Appendix. (*continued*)

	Experiment 1	*Experiment 2*
Age of acquisition	3.3 (0.6)	4.2 (0.8)
Familiarity	5.8 (1.1)	6.1 (0.7)
Imageability	3.5 (1.2)	3.9 (1.5)
State nouns	Il merito [the merit]	La temperatura [the temperature]
	L'equivalenza [the equivalence]	L'egoismo [the egoism]
	Il dispiacere [the displeasure]	Il prestigio [the prestige]
	Il bisogno [the need]	Il carisma [the charisma]
	Il desiderio [the desire]	Il sonno [the sleep]
	Il possesso [the ownership]	L'identità [the identity]
	La mancanza [the lack]	L'aspetto [the look]
	La conoscenza [the knowledge]	Il genere [the kind/genre]
	La dipendenza [the dependence]	L'affetto [the affection]
	Il timore [the fear]	L'attitudine [the aptitude]
	Il sapore [the taste]	Il nesso [the link]
	L'ignoranza [the ignorance]	La dimensione [the dimension]
	L'odio [the hate]	La qualità [the quality]
	La gioia [the joy]	La maniera [the manner]
	Il valore [the value]	La pace [the peace]
	Il costo [the cost]	L'indole [the temperament]
	L'eccellenza [the excellence]	Il calore [the heat]
	La necessità [the necessity]	La penuria [the scarcity]
	L'appartenenza [the membership]	La prerogativa [the prerogative]
	La somiglianza [the resemblance]	La particolarità [the peculiarity]
Age of acquisition	3.6 (0.7)	4.7 (0.8)
Familiarity	6.0 (1.0)	5.8 (0.9)
Imageability	3.8 (1.2)	4.0 (1.4)
Event verbs	Egli distrugge [he destroys]	Ciò arriva [this arrives]
	Egli insegue [he chases]	Ciò funziona [this works]
	Egli consuma [he consumes]	Ciò aiuta [this helps]
	Lei scrive [she writes]	Ciò avviene [this happens]
	Lei mangia [she eats]	Ciò produce [this produces]
	Lei crea [she creates]	Ciò succede [this occurs]
	Egli osserva [he watches]	Ciò prosegue [this goes on]
	Egli chiude [he closes]	Ciò gira [this spins/turns]
	Egli uccide [he kills]	Ciò accade [this happens]
	Egli racconta [he narrates]	Ciò appare [this appears]
	Egli cammina [he walks]	Ciò torna [this comes back]
	Lei piange [she cries]	Ciò bagna [this wets]
	Lei arriva [she arrives]	Ciò cambia [this changes]

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1777839/jocn_a_00257.pdf by guest on 17 May 2021

Appendix. (*continued*)

	Experiment 1	*Experiment 2*
	Egli viaggia [he travels]	Ciò causa [this causes]
	Lei corre [she runs]	Ciò coinvolge [this involves]
	Lei gioca [she plays]	Ciò trasforma [this transforms]
	Lei parte [she leaves]	Ciò scorre [this flows]
	Lei torna [she comes back]	Ciò segue [this follows]
	Lei parla [she talks]	Ciò colpisce [this strikes]
	Egli lavora [he works]	Ciò finisce [this finishes]
Age of acquisition	2.2 (0.6)	3.3 (0.9)
Familiarity	6.2 (1.1)	6.4 (0.5)
Imageability	5.9 (1.1)	4.7 (1.3)
Event nouns	La distruzione [the destruction]	Il festival [the festival]
	L'inseguimento [the chase]	La rissa [the fight]
	L'attacco [the attack]	La vacanza [the holiday]
	Il consumo [the consumption]	L'inchiesta [the inquiry]
	L'uccisione [the killing]	La scampagnata [the jaunt]
	Il ritorno [the return]	La cerimonia [the ceremony]
	Il viaggio [the journey]	La gita [the trip]
	Il pianto [the cry]	Il disastro [the disaster]
	L'uso [the use]	L'escursione [the excursion]
	La partenza [the departure]	La conferenza [the lecture/conference]
	L'arrivo [the arrival]	Il moto [the motion]
	L'esplorazione [the exploration]	Il matrimonio [the wedding]
	La corsa [the run]	Il convegno [the conference]
	La conversione [the conversion]	Il tirocinio [the training]
	La lotta [the fight]	Il funerale [the funeral]
	L'esplosione [the explosion]	L'incidente [the accident]
	La camminata [the walk]	L'imboscata [the ambush]
	Il trasferimento [the transfer]	Il pellegrinaggio [the pilgrimage]
	L'erosione [the erosion]	Il congresso [the convention]
	L'azione [the action]	Lo spettacolo [the show]
Age of acquisition	3.2 (0.6)	4.8 (0.7)
Familiarity	5.6 (1.1)	5.9 (0.9)
Imageability	5.3 (1.0)	6.0 (0.8)
Action verbs	Egli salta [he jumps]	Same as in Experiment 1
	Lei colpisce [she hits]	
	Lei combatte [she fights]	
	Lei passeggia [she walks]	
	Lei abbraccia [she hugs]	
	Egli nuota [he swims]	

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2095/1777329/jocn_a_00257.pdf by guest on 17 May 2021

Appendix. (*continued*)

	Experiment 1	*Experiment 2*
	Lei disegna [she draws]	
	Egli marcia [he marches]	
	Egli ruba [he steals]	
	Egli balla [he dances]	
	Lei rompe [she breaks]	
	Egli fugge [he runs away]	
	Lei attraversa [she crosses]	
	Egli canta [he sings]	
	Lei costruisce [she builds]	
	Lei trascina [she drags]	
	Egli beve [he drinks]	
	Egli legge [he reads]	
	Lei applaude [she claps]	
	Egli spinge [he pushes]	
Age of acquisition	2.4 (0.5)	
Familiarity	5.9 (1.5)	
Imageability	6.1 (1.2)	
Object nouns	La matita [the pencil]	Same as in Experiment 1
	La pentola [the pan]	
	La lampadina [the lightbulb]	
	La poltrona [the armchair]	
	La bacinella [the bowl]	
	La bottiglia [the bottle]	
	Il cuscino [the pillow]	
	Il quaderno [the notebook]	
	Il secchio [the bucket]	
	Lo spillo [the pin]	
	La maniglia [the handle]	
	La terrazza [the terrace]	
	Il biscotto [the biscuit]	
	La tovaglia [the towel]	
	Il cucchiaio [the spoon]	
	Il campanile [the steeple]	
	Il cassetto [the drawer]	
	Il bicchiere [the glass]	
	La camicia [the shirt]	
	Lo sgabello [the stool]	
Age of acquisition	2.1 (0.6)	
Familiarity	6.1 (1.5)	
Imageability	6.6 (1.1)	

Downloaded from http:// ... user on 17 May 2021

Acknowledgments

We thank Silvia Ubaldi for help with data collection. The research was financially supported by the Fondazione Cassa di Risparmio di Trento e Rovereto.

Reprint requests should be sent to Marius V. Peelen, Center for Mind/Brain Sciences, CIMeC, University of Trento, Palazzo Fedrigotti, Corso Bettini 31, 38068 Rovereto (TN), Italy, or via e-mail: marius.peelen@unitn.it.

REFERENCES

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4,* 267–278.

Bates, E., Burani, C., D'Amico, S., & Barca, L. (2001). Word reading and picture naming in Italian. *Memory & Cognition, 29,* 986–999.

Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., & Saxe, R. (2008). Concepts are more than percepts: The case of action verbs. *Journal of Neuroscience, 28,* 11347–11353.

Bedny, M., Caramazza, A., Pascual-Leone, A., & Saxe, R. (2012). Typical neural representations of action verbs develop without vision. *Cerebral Cortex, 22,* 286–293.

Bertinetto, P. M., Burani, C., Laudanna, A., Marconi, L., Ratti, D., Rolando, C., et al. (2005). Corpus e Lessico di Frequenza dell'Italiano Scritto (CoLFIS). Retrieved from www.istc.cnr.it/material/database/colfis/.

Burton, M. W., Krebs-Noble, D., Gullapalli, R. P., & Berndt, R. S. (2009). Functional neuroimaging of grammatical class: Ambiguous and unambiguous nouns and verbs. *Cognitive Neuropsychology, 26,* 148–171.

Campanella, F., D'Agostini, S., Skrap, M., & Shallice, T. (2010). Naming manipulable objects: Anatomy of a category specific effect in left temporal tumours. *Neuropsychologia, 48,* 1583–1597.

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,* 913–919.

Crepaldi, D., Berlingeri, M., Paulesu, E., & Luzzatti, C. (2011). A place for nouns and a place for verbs? A critical review of neurocognitive data on grammatical-class effects. *Brain and Language, 116,* 33–49.

Davis, M. H., Meunier, F., & Marslen-Wilson, W. D. (2004). Neural responses to morphological, syntactic, and semantic properties of single words: An fMRI study. *Brain and Language, 89,* 439–449.

Deen, B., & McCarthy, G. (2010). Reading about the actions of others: Biological motion imagery and action congruency influence brain activity. *Neuropsychologia, 48,* 1607–1615.

den Ouden, D. B., Fix, S., Parrish, T. B., & Thompson, C. K. (2009). Argument structure effects in action verb naming in static and dynamic conditions. *Journal of Neurolinguistics, 22,* 196–215.

Givón, T. (1984). *Syntax: A functional-typological introduction*. Amsterdam/Philadelphia: John Benjamins.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., et al. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience, 12,* 711–720.

Grossman, M., Koenig, P., DeVita, C., Glosser, G., Alsop, D., Detre, J., et al. (2002). Neural representation of verb meaning: An fMRI study. *Human Brain Mapping, 15,* 124–134.

Hauk, O., Davis, M. H., Kherif, F., & Pulvermuller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *European Journal of Neuroscience, 27,* 1856–1866.

Hopper, P. L., & Thompson, S. A. (1984). The discourse basis for lexical categories in universal grammar. *Language, 60,* 703–752.

Kable, J. W., Kan, I. P., Wilson, A., Thompson-Schill, S. L., & Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. *Journal of Cognitive Neuroscience, 17,* 1855–1870.

Kalenine, S., Buxbaum, L. J., & Coslett, H. B. (2010). Critical brain regions for action recognition: Lesion symptom mapping in left hemisphere stroke. *Brain, 133,* 3269–3280.

Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. (2012). Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex, 48,* 826–848.

Lyons, J. (1977). *Semantics* (Vol. 2). Cambridge, UK: Cambridge University Press.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology, 58,* 25–45.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science, 270,* 102–105.

Palti, D., Ben Shachar, M., Hendler, T., & Hadar, U. (2007). Neural correlates of semantic and morphological processing of Hebrew nouns and verbs. *Human Brain Mapping, 28,* 303–314.

Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron, 49,* 815–822.

Perani, D., Cappa, S. F., Schnur, T., Tettamanti, M., Collina, S., Rosa, M. M., et al. (1999). The neural correlates of verb and noun processing. A PET study. *Brain, 122,* 2337–2344.

Rueschemeyer, S. A., Glenberg, A. M., Kaschak, M. P., Mueller, K., & Friederici, A. D. (2010). Top–down and bottom–up contributions to understanding sentences describing objects in motion. *Frontiers in Psychology, 1,* 183.

Saygin, A. P., McCullough, S., Alac, M., & Emmorey, K. (2010). Modulation of BOLD response in motion-sensitive lateral temporal cortex by real and fictive motion sentences. *Journal of Cognitive Neuroscience, 22,* 2480–2490.

Shapiro, K. A., Moo, L. R., & Caramazza, A. (2006). Cortical signatures of noun and verb production. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 1644–1649.

Shetreet, E., Friedmann, N., & Hadar, U. (2010). The neural correlates of linguistic distinctions: Unaccusative and unergative verbs. *Journal of Cognitive Neuroscience, 22,* 2306–2315.

Thompson, C. K., Bonakdarpour, B., Fix, S. C., Blumenfeld, H. K., Parrish, T. B., Gitelman, D. R., et al. (2007). Neural correlates of verb argument structure processing. *Journal of Cognitive Neuroscience, 19,* 1753–1767.

Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology, 20,* 409–432.

Tyler, L. K., Bright, P., Fletcher, P., & Stamatakis, E. A. (2004). Neural processing of nouns and verbs: The role of inflectional morphology. *Neuropsychologia, 42,* 512–523.

Tyler, L. K., Randall, B., & Stamatakis, E. A. (2008). Cortical differentiation for nouns and verbs depends on grammatical markers. *Journal of Cognitive Neuroscience, 20,* 1381–1389.

Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 11656–11661.

Van Valin, R. D., & LaPolla, R. J. (1997). *Syntax: Structure, meaning and function*. Cambridge: Cambridge University Press.

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1777932/jocn_a_00257.pdf by guest on 17 May 2021

Wallentin, M., Lund, T. E., Ostergaard, S., Ostergaard, L., & Roepstorff, A. (2005). Motion verb sentences activate left posterior middle temporal cortex despite static context. *NeuroReport, 16,* 649–652.

Wallentin, M., Nielsen, A. H., Vuust, P., Dohn, A., Roepstorff, A., & Lund, T. E. (2011). BOLD response to motion verbs in left posterior middle temporal gyrus during story comprehension. *Brain and Language, 119,* 221–225.

Willms, J. L., Shapiro, K. A., Peelen, M. V., Pajtas, P. E., Costa, A., Moo, L. R., et al. (2011). Language-invariant verb processing regions in Spanish-English bilinguals. *Neuroimage, 57,* 251–261.

Wu, D. H., Waller, S., & Chatterjee, A. (2007). The functional neuroanatomy of thematic role and locative relational knowledge. *Journal of Cognitive Neuroscience, 19,* 1542–1555.

Yokoyama, S., Miyamoto, T., Riera, J., Kim, J., Akitsuki, Y., Iwata, K., et al. (2006). Cortical mechanisms involved in the processing of verbs: An fMRI study. *Journal of Cognitive Neuroscience, 18,* 1304–1313.

Downloaded from http://direct.mit.edu/jocn/article-pdf/24/10/2096/1778279/jocn_a_00257.pdf by guest on 17 May 2021