Sensorimotor experience and verb-category mapping in human sensory, motor and parietal neurons

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Abstract: Semantic grounding is the process of relating meanings to
symbols (e.g., words). It is the foundation for creating a
representational symbolic system such as language. This can be achieved
through two mechanisms: experience-to-concept mapping and concept-to-
concept mapping. We investigated these two mechanisms for concrete action
concepts in verbs at the neuronal level, by recording spike activities
from the motor, somatosensory and parietal areas in two human
participants. Motor and somatosensory neurons were found to conduct
experience-to-concept mapping primarily, while parietal and a portion of
somatosensory neurons were found to conduct both experience-to-concept
and concept-to-concept mapping. Further, the time course of neuronal
activity and the selective tuning pattern of these neurons indicate that
they belong to a large neural network used for semantic processing. This
study is the first step towards understanding how symbols are created in
the brain.

Carnegie Mellon University

Dear Editor:

Please find attached our manuscript entitled "Experience-to-Concept and Concept-to-concept mapping in Human Sensory, Motor and Parietal Neurons". To the best of our knowledge, this is the first study that investigates how individual neurons in the human brain encode meaning in language. Specifically, it tests how neurons conduct 'semantic grounding': encoding the concepts in language by relating them to real-world experiences and to each other.

We recorded single/multi-unit activities in primary motor cortex, somatosensory cortex, and superior and inferior parietal lobules while two human subjects read action verbs. We found neurons in the primary motor and somatosensory areas responded to sensorimotor aspects of action-related concepts (e.g. Body Part, or Force) directly, in a way similar to how they would respond to the sensing or execution of real actions. We also found neurons near the intraparietal sulcus that responded to more complex verb categories. These higher-level categories are derived from verb taxonomy, reflecting a similarity-based way of mapping meanings to symbols. These two mechanisms are analogous to information encoding in the human visual system pathway, which represents simple visual features in the primary visual cortex and combines them to represent complex entities, such as faces, in higher visual information processing areas. Further, we found that our neurons seem to follow the same sparse coding pattern as the "grandmother neurons" at the top level of visual pathway in the medial temporal lobe or face area (Quiroga, et al., 2005).

This is a novel study at the intersection of linguistics, single-neuron recording, and cognitive neuroscience. We consider this study of great scientific significance, as it provides the first evidence of how individual neurons in the human brain process or represent meaning in language. It will help advance the cognitive neuroscience of human language function, shedding new light on neural bases of language processing, learning and development of concepts, semantic deficits in language impairments, as well as the development of new treatment and rehabilitation strategies for communication disorders.

Having spoken with multiple linguists and neuroscientists about this work, we believe that this study will be well read and highly cited by the scientific and clinical communities. None of the submitted material has been published or is under consideration elsewhere, including the Internet. We sincerely appreciate your effort in
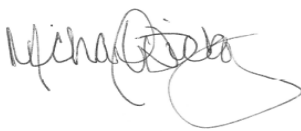
coordinating the review process, and please feel free to contact us if you have any questions or want to speak with us directly regarding this study.

Sincerely,

Ying Yang, PhD

Psychology
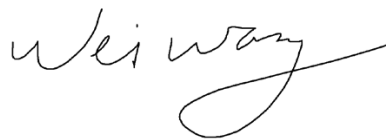Carnegie Mellon University

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Title: Experience-to-Concept and Concept-to-concept mapping in Human Sensory, Motor and Parietal Neurons

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ABSTRACT

Semantic grounding is the process of relating meanings to symbols (e.g., words). It is the foundation for creating a representational symbolic system such as language. This can be achieved through two mechanisms: experience-to-concept mapping and concept-to-concept mapping. We investigated these two mechanisms for concrete action concepts in verbs at the neuronal level, by recording spike activities from the motor, somatosensory and parietal areas in two human participants. Motor and somatosensory neurons were found to conduct experience-to-concept mapping primarily, while parietal and a portion of somatosensory neurons were found to conduct both experience-to-concept and concept-to-concept mapping. Further, the time course of neuronal activity and the selective tuning pattern of these neurons indicate that they belong to a large neural network used for semantic processing. This study is the first step towards understanding how symbols are created in the brain.

1. INTRODUCTION

Upon hearing the word 'grasp', we quickly understand the action described. In everyday language, words are used to point to real-world experiences (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). The process of establishing "meaning-to-symbol" pointers in the brain is called 'semantic grounding'. This study focuses on the grounding mechanism for concrete action verbs at the neuronal level, which informs the fundamental question of how humans map the world to language and vice versa. We tested two grounding mechanisms simultaneously, experience-to-concept mapping (Hauk, Johnsrude, & Pulvermüller, 2004: semantic concepts are grounded through direct reference to concrete sensorimotor experience) and concept-to-concept mapping (Mahon & Caramazza, 2008; Pulvermüller, 2013a: semantic concepts are grounded via knowledge of/relationships to other concepts).

Under experience-to-concept mapping, the concept in the verb "kick" may be acquired by accessing sensorimotor features like Body Part or Force in performing the action of kicking. Concept-to-concept mapping, on the other hand, requires forming taxonomies or categories, in order to use acquired concepts to learn new concepts (Kemmerer, 2006; Mahon & Caramazza, 2008; Meteyard et al., 2012; Pulvermüller, 2013a). Take the same verb 'kick' for example. It belongs to the same category as "slap" and "knock" in verb taxonomies (e.g., Levin, 1993). Verb similarity defines a high-level categorical representation that shares abstract properties common to these actions. This representation is no longer strictly tied to the specific sensorimotor experience of the action 'kick'. These two kinds of mappings have been argued to tap into two different levels of verb meanings (Kemmerer & Gonzalez-Castillo, 2010), and serve as the foundations for symbol creation.

Previous studies have indicated that these two grounding mechanisms recruit different neural networks. The experience-to-concept mapping is hypothesized to involve sensorimotor areas. Functional magnetic resonance imaging (fMRI) studies have found that action concepts modulate neural activity in somatotopically-organized motor and somatosensory areas, similar to cortical activity patterns for actual sensation or motor action (Buccino et al., 2001; Hauk et al., 2004; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; van Ackeren, Schneider, Musch, & Rueschemeyer, 2014). For example, "hand" areas responded selectively to "hand" verbs and "mouth" areas responded selectively to "mouth" verbs (Hauk et al., 2004). Magnetoencephalography (MEG) studies further show that these responses occurred earlier than

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the typical semantic processing window for words (Mollo, Pulvermüller, & Hauk, 2016). This supports the hypothesis that experience-to-concept mapping is not merely from post-comprehension processes. Rather, it may actually be a fundamental neural mechanism of concept encoding. There are also studies indicating that some aspects of action experience-to-concept mapping may also occur in associative cortices such as the inferior frontal (Barrós-Loscertales et al., 2012; Kemmerer & Gonzalez-Castillo, 2010; Moody & Gennari, 2010), temporal (Papeo et al., 2015; Romagno, Rota, Ricciardi, & Pietrini, 2012) and parietal areas (Buccino et al., 2001; Cattaneo, Maule, Tabarelli, Brochier, & Barchiesi, 2015; Fogassi et al., 2005).

Concept-to-concept mapping is also hypothesized to recruit associative cortices such as inferior frontal cortex (Bak & Chandran, 2012), temporal lobe (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Kiefer & Pulvermüller, 2012), and inferior parietal cortex (Kemmerer, 2006; Noordzij, Neggers, Ramsey, & Postma, 2008). They work in concert to activate related concepts and select the most appropriate meanings.

These neuroimaging studies have significantly advanced our understanding of semantic grounding. However, due in part to the difficulty in examining activities of individual neurons in human participants, there is still debate regarding how concepts are grounded (Arévalo, Baldo, & Dronkers, 2012) and how much experience-to-concept mapping is involved in the process (Mahon & Caramazza, 2008; Meteyard et al., 2012). First, do action concepts directly modulate firing rates of individual neurons, as actual body movement or sensation does (Georgopoulos, Schwartz, & Kettner, 1986; Wang, Chan, Heldman, & Moran, 2010)? Second, if individual neurons do respond to action concepts, what is the time window of these neuronal responses? Does this time window precede or overlap with semantic processing time windows (Kutas & Hillyard, 1980b)? Third, are these neurons "specialists" or "generalists" in semantic grounding? That is, does a neuron ground a variety of concepts, or specialize in grounding just one or two kinds?

We recorded single/multi-unit activities (i.e., spiking activities of one or a few neurons) in two human participants, from the primary motor cortex, the primary somatosensory cortex, and the superior and inferior parietal lobules near the intraparietal sulcus (shortened to 'motor units', 'somatosensory units' and 'parietal units' below). Four specific hypotheses were tested. Hypothesis I: somatosensory and motor units conduct experience-to-concept mapping only, as suggested by a theoretical framework integrating empirical studies of semantic grounding (Kemmerer & Gonzalez-Castillo, 2010). Hypothesis II: parietal units conduct both kinds of mapping, as suggested by previous studies (Aziz-Zadeh & Damasio, 2008; Cattaneo et al., 2015; Jirak, Menz, Buccino, Borghi, & Binkofski, 2010). Hypothesis III: neuronal level grounding occurs prior to the semantic processing window, consistent with previous MEG findings (Mollo et al., 2016). Hypothesis IV: each neuron specializes in grounding a very limited set of concept features or categories, since concept tuning pattern may be analogous to the tuning of other similar complex information, such as persons or objects(Anderson, Bruni, Lopopolo, Poesio, & Baroni, 2015; Quiroga, Fried, & Koch, 2013), which involves highly specialized neurons(Quiroga et al., 2013).

2. METHODS

2.1. Participants

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Participant A was a 53-year-old female with tetraplegia (Boninger, Mitchell, Tyler-Kabara, Collinger, & Schwartz, 1AD), implanted with two 96-recording-channel intracortical microelectrode arrays (Blackrock Microsystems, UT, USA) in the hand and arm areas of the left primary motor cortex for a neuroprosthetic study (Collinger et al., 2013). Participant B was a 28-year-old male with a C5 level spinal cord injury,implanted with four arrays: two 96 -channel arrays in the somatosensory area and two 32-channel arrays in the superior and inferior parietal lobules respectively, near the intraparietal sulcus (Blackrock Microsystems), also for a neuroprosthetic study. Figure 1A shows the locations of the microelectrode arrays.

2.2.Video-following task

Videos with different hand movements were shown to the participants on the same days they completed the verb-reading task. An example is shown in Figure 1B. The red dashed lines indicate the kinematics of the videos. The participants were instructed to watch these videos and "attempt" to perform these movements in their mind, in time with the videos. These videos were made to test directly whether neurons that code physical actions or sensations can also map these experiences to verbs.

2.3.Verb-reading task

The participants read 400 concrete action verbs silently following the paradigm shown in Figure 1C. Each verb was shown for one second with an inter-stimulus interval of one second. The participants were instructed to read the verbs naturally, without any explicit sensorimotor imagination/rehearsal. Catch trials (7% of the total trials), requiring participants to make a sentence using the immediately previous verb, were randomly interleaved to ensure that the participants paid sustained attention to the verb's meaning.

-----------------Figure 1 about here----------------------

Figure 1 The microelectrode array locations and the experimental paradigm. *1A*: Array locations of the two subjects, registered on their respective MRI scans. **Left**: Subject A, one array was implanted in the finger area of the primary motor cortex (precentral gyrus, labeled 'F') and another was in the hand area (labeled 'H'). Both arrays have 96 recording channels. CS: central sulcus. **Right**: Subject B, two square arrays (96 recording channels) were implanted in the primary somatosensory area (postcentral gyrus, labeled 'S') while another two rectangle arrays (32 recording channels) were placed on superior and inferior parietal lobules, respectively (labeled 'P'). IPS: intraparietal sulcus. *1B*: Experimental Paradigm for the verb reading tasks: videos with different hand, wrist, elbow and shoulder movements were shown to the subjects to map sensorimotor cortex responses on the same day of recording verb reading paradigm. These videos were made following the same timeline: consisting of one second of movement and two seconds of holding. Each whole video consisted of five such repetitions. An example was shown here. The red dashed line indicated the kinematics of index finger. Both subjects were instructed to watch all of the videos and make efforts to 'attempt' the movements in the video as if they could perform them, with the same pace of the video. *1C*: Experimental Paradigm for the verb reading tasks: the subjects were instructed to read verbs silently. The verbs were presented for 1 second with an inter-stimulus interval of 1 second. Catch trials were included to keep the subjects attentive. In a catch trial, they were cued to make a sentence with the verb just shown.

2.4.Semantic features and categories

To quantify experience-to-concept and concept-to-concept mapping, stimulus verbs were coded based on seven experience-related sensorimotor features (Body Part, Object, Duration, Boundedness, Force, Decomposability, and Complexity) by three human specialists in linguistics. They were also categorized into one of the branches of an independent verb taxonomy (Levin, 1993) so as to quantify their similarities to other verbs (the categories are: [MIX], [REMOVE], [SEND/BRING], etc.). Selected examples are in Table 1. For more detailed references and examples, please refer to the Supplemental Materials.

2.5. Recording Setup

Spiking events crossing a threshold (-4.5 times the root-mean-square (RMS) value of the noise floor for Participant A and -5.25 RMS for Participant B) were recorded by NeuroPort data acquisition system (Blackrock Micro systems) and synchronized with video or verb presentations through digital input. Single- and multi-unit activities were sorted manually offline (CentralPlay, Blackrock Micro systems, see Supplemental Materials for the unit sorting procedure).

3. RESULTS

To test Hypotheses I-III, the modulation of instantaneous neuron firing rates was examined by attempted movements from the video-following task and concept features/categories in the verb-reading task. Then, we examined whether the variances of neuron firing rates can be explained by the coded sensorimotor features or verb categories at the unit level in regression models. To test Hypothesis IV, a tuning pattern analysis was also conducted, to determine which and how many kinds of semantic concepts each unit was tuned to.

3.1. Firing Rate Modulation

To examine whether neuronal firing rates are directly modulated by the video-following and verb-reading tasks, firing rates were plotted against kinematics of the video and verb features for each unit. Three prototypical units from the motor, somatosensory and parietal areas were shown in Figure 2. The firing rates of these units were modulated by the attempted movements when the participants were watching the index finger flexion video. Furthermore, the same units were modulated by a sensorimotor feature of action verbs (Duration). This indicates that these units mapped sensorimotor experiences (duration in the videos) to action concepts (duration concept in verbs). Units that showed modulations to the concept categories were also found; see the Supplemental Materials for their spike-rate modulation plots.

--------------------Figure 2 about here---------------------------------

Figure 2. Firing rates of three prototypical units from motor, somatosensory and parietal areas responded to sensorimotor tasks (top) and verb reading tasks (bottom). For the top figure, the blue curve is the averaged firing rates of the unit over 5 repetitions. In each repetition, subjects were watching the video of index finger flexion, and attempted in her/his mind to do the actions following the same pace in the videos. The red dashed line traced the kinematics of the video. It can be seen that these units locked their firing activities to the kinematics of the videos. For the bottom figure, grey dash lines indicate stimulus onsets, and the two colors indicate verbs with different values of the sensorimotor feature *Duration*. Specifically, the red curve indicates the averaged firing rates over 245 durative verbs (e.g. breathe, swim), and the blue curve indicates the averaged firing rates over 155 punctual verbs (e.g. grasp, knock). It can be seen that this unit showed higher firing rates of durative verbs over punctual verbs. In other words, it responded to the sensorimotor feature of *Duration*.

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3.2. Unit-level mapping

We regressed neuronal firing rates for each unit against the sensorimotor features or concept categories for action verbs in a sliding-window fashion (200ms window and 30ms step). This regression model assessed systematically whether the variances of neuronal firing rates could be explained by these two kinds of mappings. If the unit-level encoding model was significant within a given time window (corrected for multiple comparisons), this window was defined as a *significant encoding window*. Units with significant encoding windows were defined as *tuned units*. The p-values of tuned units in all the time windows are shown in Figure 3. Overall, 74 units from the motor cortex (38% of units), 28 units (40%) from the somatosensory cortex, and 32 (55%) units from the parietal area were tuned to sensorimotor features. Seven (10%) units from the somatosensory and twenty-five (43%) parietal units showed significant tuning to verb categories. The number of motor units that showed tuning to verb categories was so small (five) that it may be attributable to chance (Benjamini & Hochberg, 1995). It can also be seen that the encoding time windows of tuned units were widely distributed, extending both before and after the canonical semantic processing window (Kutas & Hillyard, 1980a).

We also investigated how many units conducted experience-to-concept mapping across domains, responding both to the video-following and verb-reading tasks. We found that a significant portion of the units were 'bimodal' in this sense: 30 units (41%) from motor cortex, 10 units (36%) from somatosensory cortex and 7 units (22%) from parietal area.

----------------Figure 3 about here------------------------

Figure 3. Unit-level encoding model. **Left Column**: neural firing rates regressed against the sensorimotor features, indicating whether each individual neuron conducts experience-to-concept mapping; **Right Column**: neural firing rates regressed against verb-concept categories, indicating whether each individual neuron conducts concept-to-concept mapping. **Top row**: motor units; **middle row**: somatosensory units; **bottom row**: parietal units. In all figures, the units were sorted by the temporal order of their significant encoding windows. The white dashed line indicated the onset of the stimuli. The color scales were the same: red and orange colors indicated significance of the encoding model. The p-value for each window was plotted at the window center. Therefore, the earliest significant encoding window occurs around 100ms post stimulus onset, though it seems like right at the onset on the figure.

3.3. Tuning Properties of Neurons

To tease apart the contribution of each sensorimotor feature/verb-concept category, the number of units tuned to each feature/category was counted. The results are shown in Figure 4. The percentage distributions for sensorimotor features were plotted in the left column of Figure 4A for motor, somatosensory and parietal units, respectively. Units were distributed evenly among the features in motor and somatosensory neurons, except for Force. In contrast, the two most tuned features were Duration and Force in the parietal cortex. The percentages of units tuned to the different verb categories were plotted in the right column of Figure 4A. Seven verb-concept

categories (out of 12) had a significant number of units tuned to them. For the motor units, none exceeded chance level. For the somatosensory units, three verb categories exceeded chance level: [REMOVE], [SEND/BRING], and [MIX]. For parietal units, four exceeded chance level: [PUT], [GIVE/EQUIP], [THROW], and [PERFORM]. Figure 4B shows the histogram of the number of features/categories that units were tuned to.

-----------------------Figure 4 about here----------------------

Figure 4. Tuning Patterns. *4A:* upper row: percentage of tuned units to each sensorimotor features; lower row: percentage of tuned units to each of the seven verb-concept categories that yield significant tuning windows. The left column: motor units; middle column: somatosensory units; right column: parietal units. Sensorimotor features: Dr-Duration, Bd-Boundedness, Ob-Object, Bd- Body Part; Cp-Complexity, Dp-Decomposability, Fc-Force. Verb-concept categories: [P]: [put] verbs; [R]: [remove] verbs; [S/B]: [SEND/BRING] verbs; [G/E]: [GIVE/EQUIP] verbs; [T]: [THROW] verbs; [M]: [MIX] verbs; [PF]: [PERFORM] verbs. Red dashed line indicated significance level. *4B*: the number of units tuned to one, two, three or four semantic features. Most units tuned to only one or two features.

Sensorimotor features are not independently distributed in verbs (due to the physical constraints of outside world, e.g. punctual actions usually have a boundary). Because of this systematic covariance, we analyzed whether these correlations can be seen in the tuning patterns of the neurons. Specifically, we checked whether the units tuned to more than one sensorimotor feature grouped these correlated features together. Such a pattern did indeed appear. First, highly correlated feature pairs tend to have more tuned units than less correlated feature pairs (r=0.35, p=0.06). Second, the largest group of "combination units" was tuned to 'Duration' and 'Boundedness'. This co-occurrence may be attributed to the fact that the majority of punctual actions also have a physical boundary, and these neurons specifically tuned to "punctual actions that have a physical boundary." Therefore, these "combination neurons" may still be "specialists" rather than "generalists", i.e. they were tuned to the specific "interfaces" between pairs of features that usually occur together in the physical world. Please refer to the Supplemental Materials for the complete correlation analyses tables.

4. DISCUSSION

Overall, we found that neurons in the motor, somatosensory, superior and inferior parietal lobules selectively responded to sensorimotor features or verb-concept categories when human participants silently read action verbs. Further, their tuning properties followed a trend: gradually decreasing representation of experience-to-concept mapping and increasing representation of concept-to-concept mapping, moving from primary motor to somatosensory to superior/inferior parietal lobules. Because the participants were instructed not to attempt or imagine actions described in the verbs, tuning to sensorimotor features in motor and somatosensory neurons is consistent with our hypothesis regarding experience-to-concept mapping: semantics related to

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real-world experiences prompts the same neuronal response as performing or sensing a movement.

Also as expected, the verb-concept category taxonomies were processed in neurons near the intraparietal sulcus. This is consistent with our hypothesis about parietal neurons' role in associative semantic processing. In addition, the significant verb-concept categories aligned well with the general cognitive bias of the parietal area: spatial trajectory processing or action planning (Culham & Kanwisher, 2001). For example, [THROW] verbs generally involve a spatial change of location, while [GIVE/EQUIP] and [PERFORM] verbs involve complex action planning. Because the verb-concept categories can be viewed as a high-level taxonomy derived from abstraction over sensorimotor experiences, our results also suggest how heteromodal semantic representations may emerge from sensorimotor information.

Unexpectedly, some somatosensory neurons were also tuned to verb-concept categories, though to a much lesser degree than parietal neurons. There are two possible interpretations of this result. First, it is possible that verbs in the same taxonomy category do share some similar sensory information (e.g. verbs in the [THROW] category may share the sensory information of "quickness"), and these neurons process this shared similarity. Second, somatosensory neurons may receive top-down input from superior/inferior parietal lobules as part of concept-to-concept mapping circuits, as discussed in the literature on mirror neurons (Pineda, 2008).

The tuning time window distributions covered the whole time span of pre-comprehension and post-comprehension processes. This broad time coverage, across the neuronal population, indicates that different neurons may participate in different stages of semantic comprehension: some units' response time windows correspond to the earliest stage of semantic comprehension: activating all the related meanings of the current stimulus (100-250ms) (Greenwald, Draine, & Abrams, 1996). Some corresponds to the stage of selecting the best-fitted meaning (250-550ms) (Lau, Phillips, & Poeppel, 2008). Finally, some late-responding neurons may contribute to post-comprehension processes, such as priming the sensorimotor system *after* a related concept is comprehended (Mahon & Caramazza, 2008; Pulvermüller, 2013b).

We did not observe differences in time windows between experience-to-concept mapping and concept-to-concept mapping. This suggests that accessing the two kinds of semantic information might be parallel processes in the brain: there is no strict temporal order of processing these two mappings. The broad time coverage also suggests that these areas may belong to a larger semantic network, constantly sending and receiving sensorimotor or verb-concept category information among different regions/processes (Papeo et al., 2015; Romagno et al., 2012).

Interestingly, the neurons were all very selective in grounding semantics: they responded to one or only a few features/categories. This is analogous to sparse coding seen in the high-level visual system (Vinje & Gallant, 2000). Further, the neural encoding to sensorimotor experiences may also adapt to the physical constraints of the real world. For example, for neurons that are tuned to two sensorimotor features, these features are most likely to be correlated between themselves.

Though selective to the semantic features they respond to, the neurons may not be selective to input modalities. Some neurons are bimodal: they process both actual sensorimotor experience, and experience-to-concept mapping. A previous fMRI study failed to find such correspondence in the BOLD signals (Postle, McMahon, Ashton, Meredith, & de Zubicaray,

2008). The difference between this study and the current study lies in the different spatial resolution scales. The bimodal neurons in the current dataset did not form any spatial clusters, i.e. they usually are not neighbors to each other. This may lead to the observation of bimodal neurons at the microscopic rather than the macroscopic level. The question of why there are both unimodal and bimodal neurons and the implications of this organization for language learning and evolution needs further study.

In summary, this study has three main findings. First, action concepts associated with verbs directly modulated neuronal activities in three different areas (primary motor, somatosensory and superior/inferior parietal lobules) of two human participants. Since our task, natural reading, is a highly automatic process in adult readers (Rayner, 1998), it is reasonable to conclude that semantic grounding by these neuron populations occurred naturally as well. Second, this study identified the type of concept mapping associated with each area. Experience-to-concept mapping was represented in decreasing degree from motor/somatosensory to parietal areas, whereas concept-to-concept mapping was represented in increasing degree across these areas. This trend is consistent with a hierarchical semantic processing mechanism, moving from more specific to more abstract semantic representations. Third, the study characterized the encoding time window distribution and tuning properties for semantic grounding at the neuronal level. Neurons were very selective for the concepts/features they were tuned to, and the populations had broad tuning time coverage. Both the broad time coverage and the selective responsiveness suggest that these areas are active members of a larger semantic network for concept processing.

Overall, the results of the current study agree with a weak version of the 'embodiment' theory (Mahon & Caramazza, 2008; Meteyard et al., 2012), in that sensorimotor experiences may be processed by both sensorimotor regions and associative regions, and only a portion of the experience encoding neurons also conduct concept mapping.

The current study does have limitations that need to be acknowledged. First, due to the small sample size of the participants, the neural region differences found in the current study may be attributed in part to participant differences. Additional data from other participants are needed to test this possibility. Second, nonsense word control stimuli may be included in future studies, to further validate that the semantic grounding reported here was indeed specific to real words. Third, as a first-step estimation of concept-to-concept mapping, the verb taxonomy (i.e. Levin's, 1993, verb-concept categories) may not necessarily be the best neural implementations of concept-to-concept mapping mechanisms. More realistic and neural-based category mapping features still need to be explored.

This study provides the first set of evidence regarding how individual neurons in the human brain represent meaning in language. These findings can be helpful in developing theories of neural symbol creation: how the neurons developed for other cognitive tasks are "repurposed" to represent symbols. It could potentially boost advancement in areas of neurobiology of language processing, learning and development. Further, it could inform treatment of semantic processing deficits in aphasia (Engelter et al., 2006) and semantic dementia (Kim & Thompson, 2004), by revitalizing or augmenting impaired mapping mechanisms (Boo & Rose, 2011).

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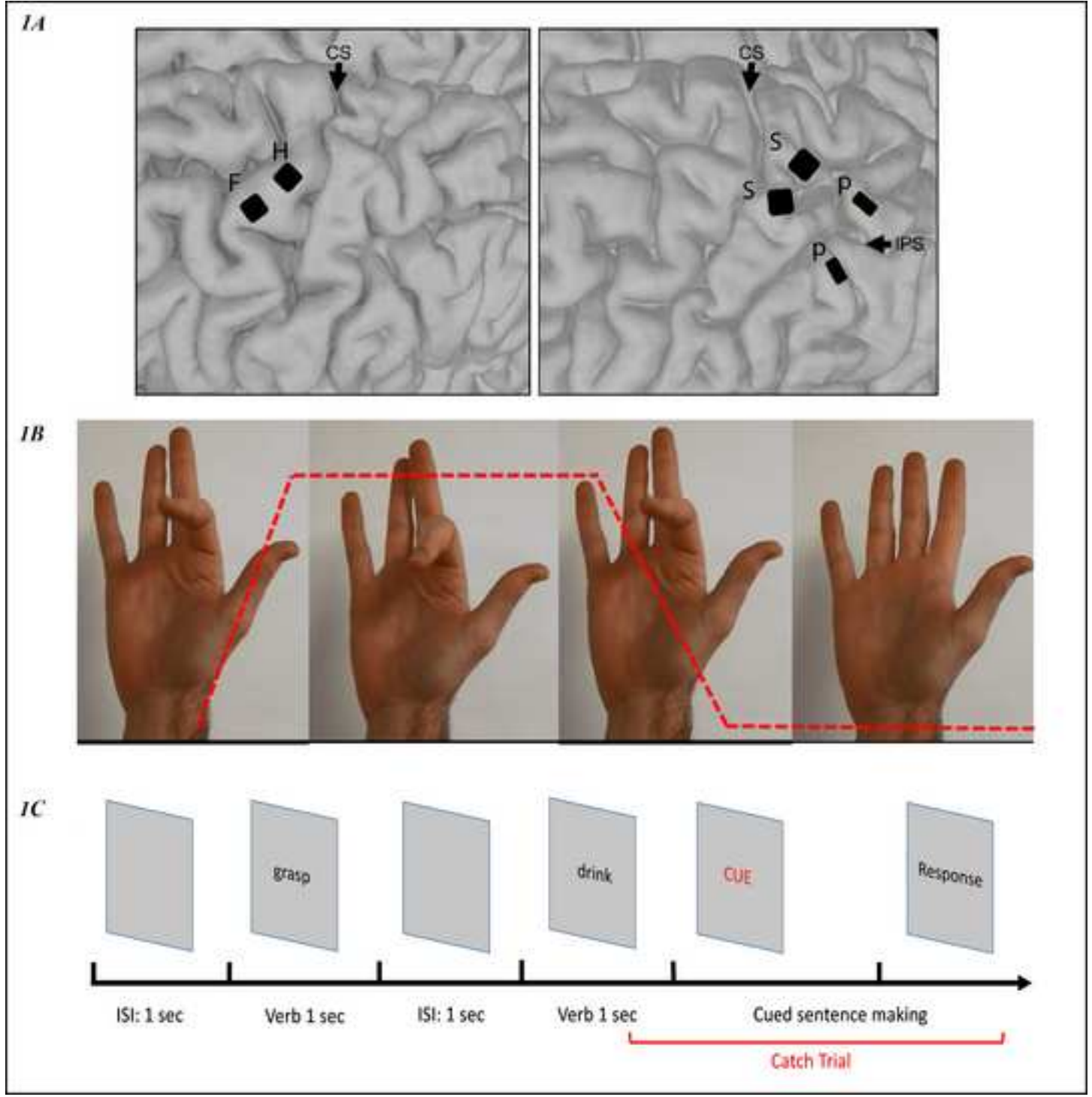
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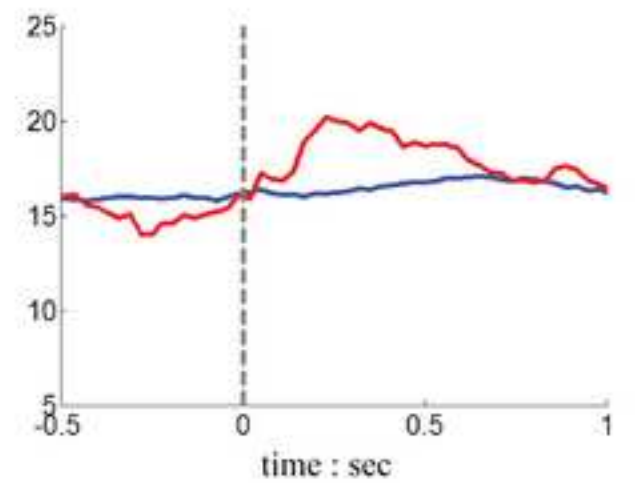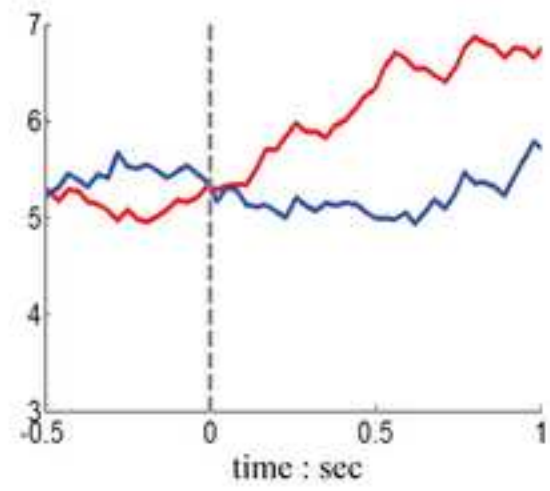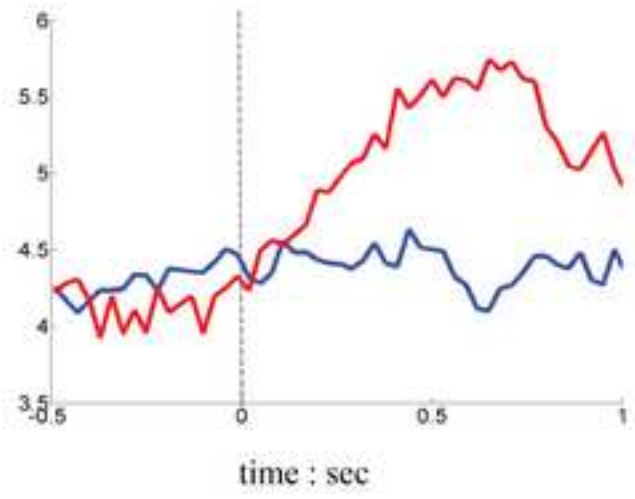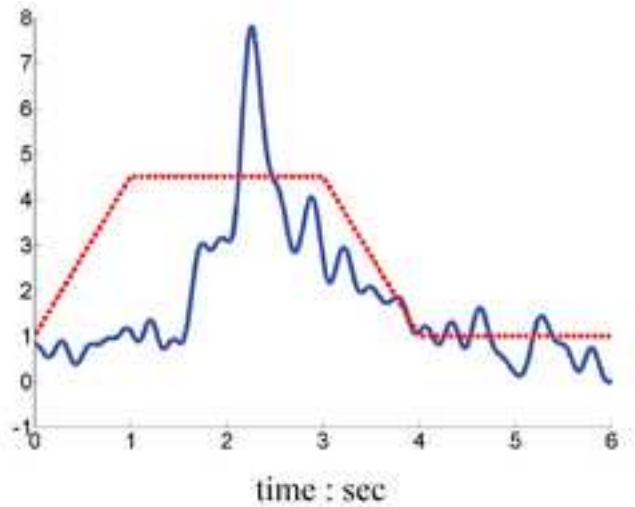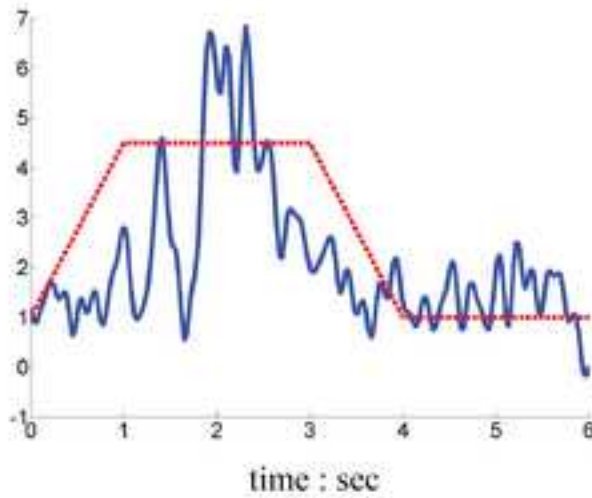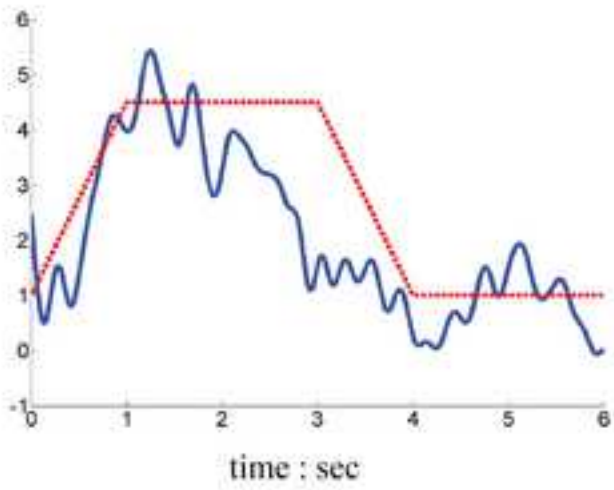
1A

1B

1C

ISI: 1 sec   Verb 1 sec   ISI: 1 sec   Verb 1 sec   Cued sentence making

Catch Trial

graso   drink   CUE   Response

Experience-to-concept mapping | Concept-to-concept mapping

Motor Units

Somatosensory Units
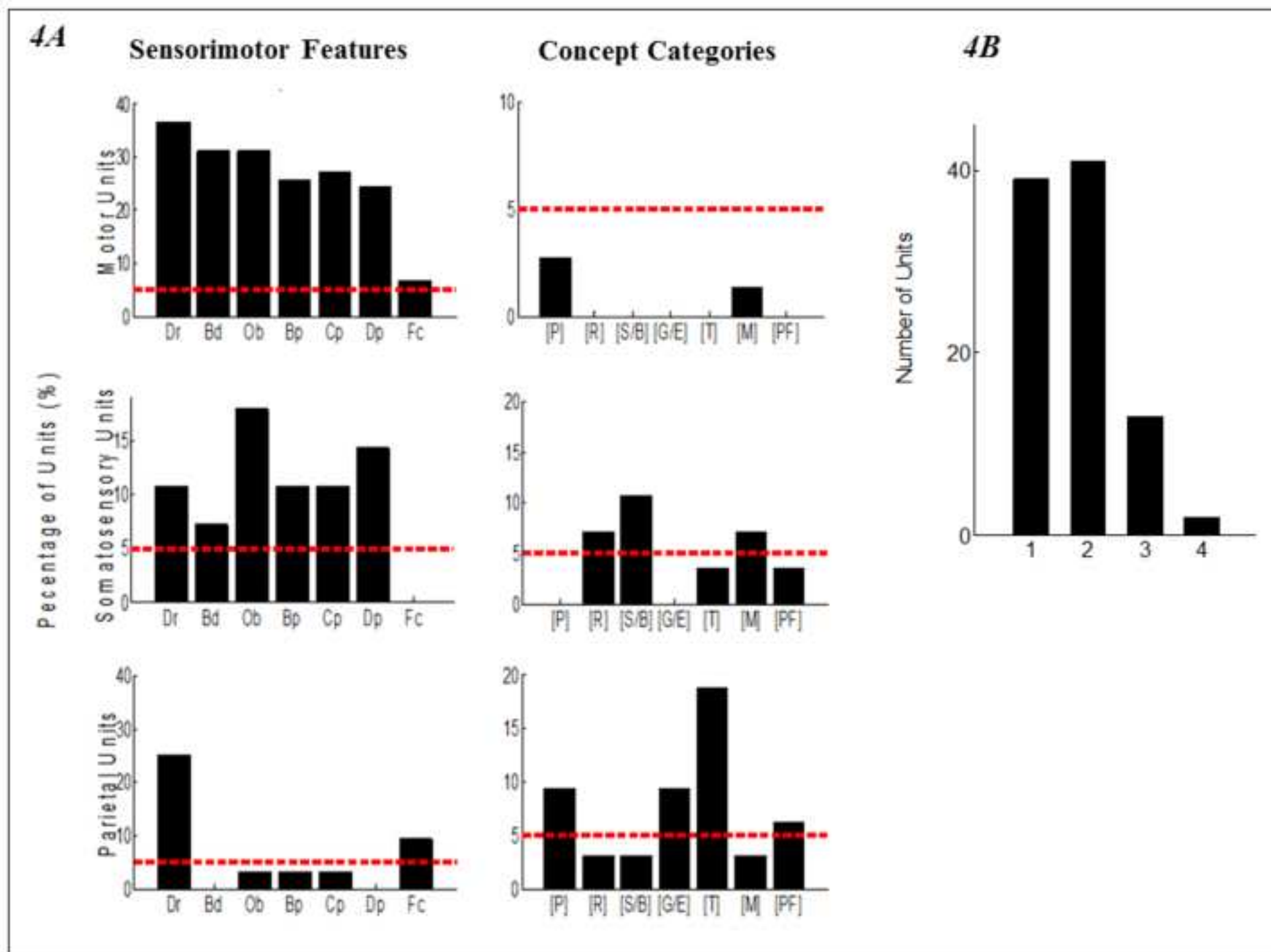
Parietal Units

Time: Seconds
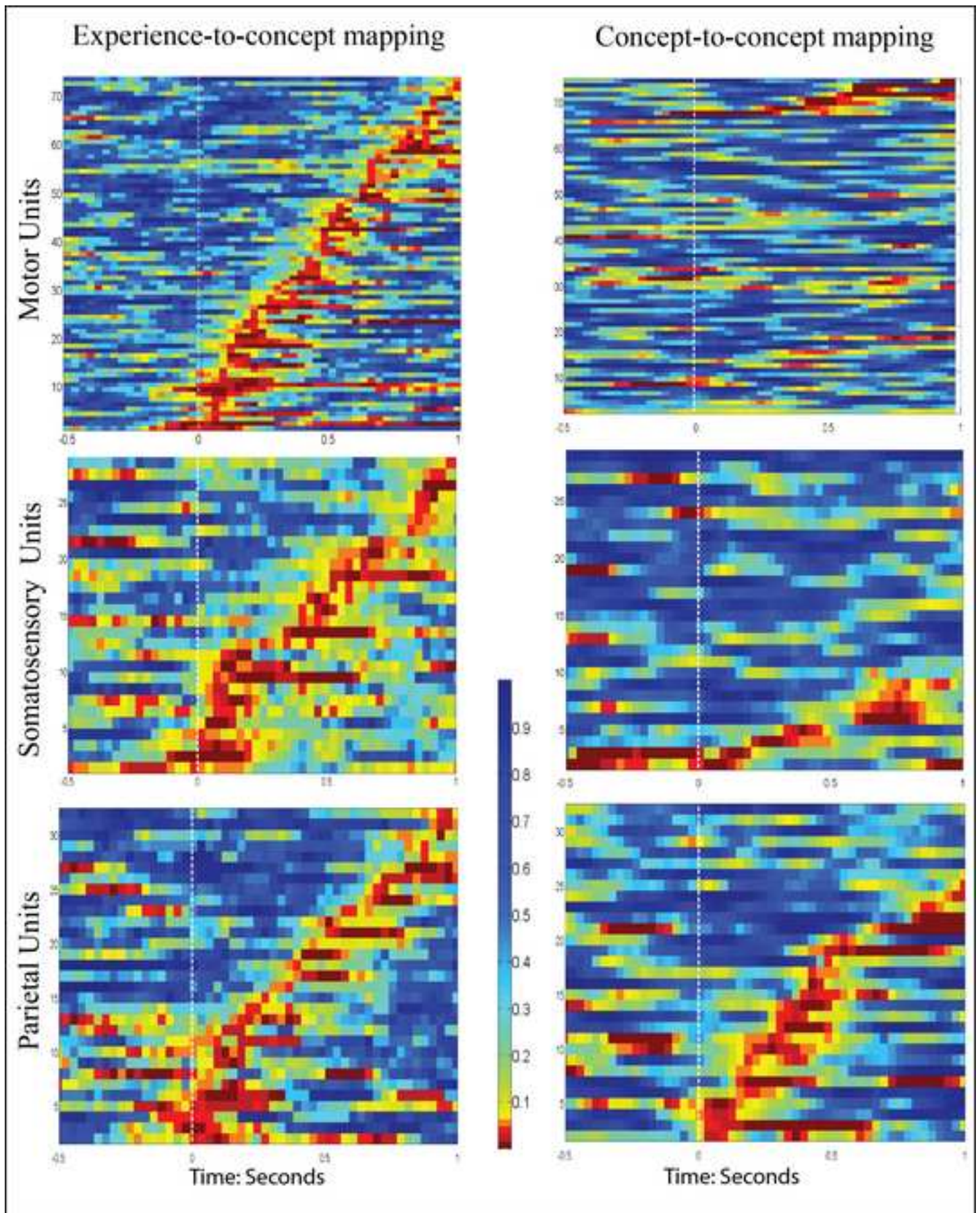
Table 1. Each verb was parameterized into seven sensorimotor features and categorized into one of the verb-concept categories. Example verbs are shown below. *Sensorimotor Features:* **Duration**: whether the action is continuous or punctual, coded 1 for durative verbs and 0 for punctual verbs; **Boundedness**: whether the action has a definite end, coded 1 for boundary presence and 0 for absence; **Object**: whether the action involves manipulating an object, coded 1 for requiring objects and 0 for not requiring objects; **Body Part**: whether hand is involved, coded 1 for involving hand, and 0 for not; **Complexity**: whether the action involves complex movement sequences, coded 1 for complex and 0 for simple; **Decomposability**: whether the action can be decomposed in sub-actions, coded 1 for yes and 0 for no; and **Force**: how strong a force the action requires, coded 1 for verbs with weak force, coded 2 for verbs with intermediate force, coded 3 for strong verbs and coded 0 for non-force related verbs. *The verb-concept categories:* extracted from Levin (1993).

Example verbs	grasp	breathe	knock
Sensorimotor Features			
Duration	0	1	0
Boundedness	1	0	1
Object	1	0	1
Body Part	1	0	1
Complexity	1	0	1
Decomposability	1	1	1
Force	3	1	2
Verb-concept categories			
Category No. definition	15 [hold]	40 [breathe]	18 [hit]