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The effects of an action's "age-of-acquisition" on action-sentence processing☆,☆☆

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ABSTRACT

How does our brain allow us comprehend abstract/symbolic descriptions of human action? Whereas past research suggested that processing action language relies on sensorimotor brain regions, recent work suggests that sensorimotor activation depends on participants' task goals, such that focusing on abstract (vs. concrete) aspects of an action activates "default mode network" (rather than sensorimotor) regions. Following a Piagetian framework, we hypothesized that for actions acquired at an age wherein abstract/symbolic cognition is fully-developed, even when participants focus on the concrete aspects of an action, they should retrieve abstract-symbolic mental representations. In two studies, participants processed the concrete (i.e., "how") and abstract (i.e., "why") aspects of late-acquired and early-acquired actions. Consistent with previous research, focusing on the abstract (vs. concrete) aspects of an action resulted in greater activation in the "default mode network". Importantly, the activation in these regions was higher when processing later-acquired (vs. earlier acquired) actions—also when participants' goal was to focus on the concrete aspects of the action. We discuss the implications of the current findings to research on the involvement of concrete representations in abstract cognition.

Introduction

Much of human activity revolves around communicating with other humans using the symbolic form of language; and a large portion of human linguistic-symbolic communication entails an exchange of information concerning the actions of other humans (Dunbar, 2004). This exchange of information concerning human actions plays an important role in shaping our behavior; for example, if you are told that "Donald stole the candy from the baby's mouth", you may be less likely to vote for Donald for presidency. How does our brain allow us to comprehend and respond to such abstract and symbolic descriptions of human action? In recent years, two major alternatives have been suggested.

According to the "embodied cognition" framework (e.g., Barsalou, 1999; Niedenthal et al., 2005), humans' ability to understand action sentences is dependent on the retrieval of concrete sensory and motor representations. In a nutshell, this account suggests that in order to decipher the meaning of an abstract message such as "Donald stole the candy", we must re-create the concrete perceptual and motor experiences associated with taking candy from a baby (for example, imagining grabbing the lollipop and overpowering the baby in a tug o' war; then gleefully running away, blonde hair scattered by the wind). Furthermore, embodiment theory suggests that humans are able to re-create these perceptual and motor states by re-activating neural systems that are involved in actual action and perception (e.g., Barsalou, 1999).

Indeed, much neuroscientific research has been brought forth to support these predictions. For example, research has shown that motor verbs (e.g., Hauk et al., 2004) and sentences (e.g., Tettamanti et al., 2005) activate the motor cortex in a somatotopic manner (i.e., hand-related words activate regions associated with hand movement, leg-related words activated regions associated with leg movement, and so forth). Furthermore, some neuropsychological evidence likewise suggested that the motor cortex may play a causal role in processing action-related semantics; for example, lesions to hand-related motor-primary motor cortex regions were shown to be associated with disrupted processing of action-related semantics using a stimuli set that included mostly hand-related sentences (Kemmerer et al., 2012).

However, it is important to note that the role of the motor system in action language processing remains under considerable debate. For example, a meta-analysis of action language processing did not find statistically significant activations in premotor and primary motor cortex regions (Watson et al., 2013). Furthermore, it has been shown that

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non-words can produce reliable activation in primary and premotor cortex regions, and that motor activation during action word processing may stem from the computation of ortho-phonological properties that are involved in deciphering grammatical classes (de Zubicaray et al., 2013). Finally, a study investigating the consequences of lesions to effector-specific motor regions did not find evidence for effector-specific semantic impairments (Arevalo et al., 2012).

In contrast to embodied cognition theory, traditional accounts of human cognition (e.g., Fodor, 1983) have long argued that the neural and cognitive systems that are responsible for abstract cognition—as the type involved in language comprehension—are functionally segregated from the systems that are responsible for processing concrete sensory and motor experiences. These views are supported by much research (e.g., Binder et al., 2009; Stephens et al., 2010) that shows that processing linguistic-symbolic meaning activate a set of regions that include the ventromedial prefrontal cortex (vmPFC), dorsomedial prefrontal cortex (dmPFC), lateral temporal cortex, temporo-parietal junction (TPJ), posterior cingulate cortex (PCC), and superior frontal gyrus, often collectively referred to as "the default mode network" (Raichle et al., 2001). This network of regions is also recruited when thinking about people's goals and mental states (e.g., Frith and Frith, 2006; Van Overwalle, 2009; Spunt et al., 2011), as well as in other abstract cognitive tasks such as considering future (e.g., Schacter et al., 2007; Gilead et al., 2013b) and counter-factual events (e.g., Van Hoeck et al., 2012). Importantly, this network has very little to no overlap with the neural systems that subserve sensorimotor processing. As such, these findings were taken to support the hypothesized classic distinction between abstract/symbolic cognition and concrete/sensory-motor cognition (e.g., Binder et al., 2009).

In an attempt to integrate the theorizing and research in "classic" and "embodied" theories of semantics, recent work has shown that when people focus on the concrete aspects of an action (e.g., think about "*how* Danny ate the bread"), they indeed activate sensory and motor regions; however, importantly, this is not the case when they focus on the more abstract aspects of the *same* action (e.g., think about "*why* Danny ate the bread"). Instead, when individuals focus on abstract aspects of the action they consistently and robustly activate the "default mode network" regions involved in social-cognitive and linguistic-symbolic processing (Spunt and Adolphs, 2014; Spunt et al., 2010, 2011; Spunt and Lieberman, 2012, 2013; Gilead et al., 2013a). Thus, according to this line of findings, the retrieval of sensory-motor representation may not be a necessary part of language comprehension, but rather, is dependent on the goals and processing mode of the perceiver.

In the current research we wish to build on this prior work (e.g., Spunt and Adolphs, 2014; Spunt et al., 2010, 2011; Spunt and Lieberman, 2012, 2013; Gilead et al., 2013a) and go one step forward, to suggest that for some actions, focusing on *concrete* aspects still calls upon *abstract*-symbolic mental representations. This is because many human actions are so intertwined with their symbolic significance, such that trying to think of the concrete aspects of these actions will nonetheless bring to mind abstract representations. Specifically, we suggest that one dimension that plays an important role in determining whether an action is represented abstractly or concretely is the age at which the person learned about this action.

Consider the case of a child learning to play drums at the age of six. In the terminology of the Piagetian framework (e.g., Inhelder and Piaget, 1958) this child is still in the "preoperational stage" of cognitive development: his/her symbolic thinking capacities have still not completely developed, and s/he is likely to focus on the concrete, sensory-motor properties of drum playing. However, if this child learns how to play the drums at the age of twelve (i.e., in Piagetian terms, a child that has passed the "concrete operational stage", and can now perform abstract, "formal operations"), the acquisition of drum-playing behavior is likely to recruit more abstract cognition. For example, at this later age s/he is more likely to focus on the more abstract social significance of the action (it makes me look cool, it is part of my overarching goal to become a musician) and rely on symbolic representations to learn the skill (e.g., follow explicit rules and musical notation). Because of these major differences, it is possible that when one learns to play the drums at a later (rather than earlier) age, the abstract aspects of drum-playing become part and parcel of the mental representation of this action. Likewise, "drinking juice", an action likely acquired at an early age, can perhaps be processed without bringing to mind any abstract and symbolic meaning. In contrast, "drinking beer", is likely to be acquired at an age at which a person would be already aware of its symbolic meaning in the social world. As a consequence, one's knowledge concerning this action may be inseparable from more abstract cognitive processing.

Based on this reasoning, we suggest that even when people consider "how" later-acquired actions are performed, they will nonetheless tend to process the abstract significance of this action—as indexed by the elevated degree of activity in neural regions that are typically recruited in processing abstract aspects of actions (namely, the regions that are typically activated when participants think "why" an action is performed).

The notion according to which "age-of-acquisition" could play an important role in cognitive processing has been supported in research showing that early-acquired words are processed more quickly than later-acquired words (e.g., Turner et al., 1998), possibly due to their greater familiarity/frequency (Lewis et al., 2001) or greater imageability (Wilson et al., 2013; but see Izura et al., 2011). Furthermore, theories of the structure of semantic networks (e.g., Steyvers and Tenenbaum, 2005) suggest that our semantic system may be built in a hierarchical manner, such that later-acquired semantics are built on the scaffolds of earlier-acquired semantics. However, despite the recognition of the importance of age-of-acquisition in research into lexical and semantic processing, previous work has not investigated how the age of acquisition of an action affects the processing of action sentences—and whether the age of acquisition of an action moderates the degree to which action sentence processing relies on concrete vs. abstract mental representations.

In order to investigate these questions we conducted two studies in both of which participants focused on the concrete (i.e., "how") vs. abstract (i.e., "why") aspects of actions that they acquired relatively earlier or later in life. Consistent with previous work, we predicted that default network activity will be relatively higher when participants thought about "why" (vs. "how") an action is performed. Furthermore, and most importantly, we predicted that default network activity will be higher for later-acquired (vs. earlier-acquired) actions, regardless of whether participants focused on "how" or "why" an action is performed.

Methods

Stimulus ratings

We created a list of 100 behaviors by complementing a verb with two different objects. The stimuli were constructed such that one of the verb-object pairings described a behavior that we suspected would be acquired at a relatively younger age (i.e., "scratching a *mosquito's bite*") and the second verb-object pair described a behavior that we suspected would be acquired later in life (i.e., "scratching *a lottery ticket*"). We used extensive pre-testing to establish the supposed differences in age of acquisition between the two groups of verb-object pairs. In the pre-test, we also obtained ratings on seven potential correlates of age of acquisition, such as familiarity, imageability and complexity.

In the pre-test, forty psychology students from Tel-Aviv University rated the stimuli along eight different dimensions. They provided an estimate of the age in which they first performed the described activity. In case they had never performed the activity they did not specify the age of acquisition. Participants also rated the activities along the following dimensions: frequency of performing the activity (1 = at least once a day, 5 = never); the degree to which they are able to imagine the activity (1 = with no difficulty, 5 = with much difficulty); degree of familiarity with the activity (1 = highly familiar, 5 = highly unfamiliar); how enjoyable is the activity (1 = highly un-enjoyable, 5 = highly enjoyable); and the degree of motor, social, and cognitive complexity of the activity (each rated on a scale of 1 = very easy, 5 = very difficult). For example, the cognitive complexity items asked participants: "to what extent do you find this activity difficult to perform—because of the degree to which it is cognitively complex and demanding?". Each participant rated an average of 30 activities randomly selected from the list of 100, on each of the 7 dimensions. Each activity received between 10 and 20 ratings on each of the dimensions, with an average of approximately 13 ratings.

Outline of studies

The pretest revealed several systematic differences in the ratings of late-acquired (LA) and early-acquired (EA) behaviors (see Table 1). Activities that were acquired later in life were rated by our pre-test participants as more cognitively complex, less familiar, more frequent, and harder to imagine. There are two ways to view these differences: first, as natural correlates of age of acquisition, and second, as unnecessary confounds of this dimension. If Default-Mode Network activity is higher when processing LA vs. EA behaviors, it is interesting to examine whether differences in activation emerge only when age of acquisition co-occurs with complexity, familiarity, frequency and imageability, or whether they emerge also when these factors are controlled for. Our two studies aimed at answering this question.

Specifically, Study 1 made use of stimuli that gave rise to the most marked difference in age of acquisition, but preserved the differences between early-acquired and late-acquired actions in complexity, familiarity, frequency and imageability; Study 2 made use of stimuli that were equated along all other dimensions, which gave rise to a smaller difference in age of acquisition.

Another important element of the current experimental design is that each stimulus was processed under both task conditions (focusing on mental, "why" aspects of the action vs. focusing on physical, "how" aspects of the action). As noted earlier, past research shows that the processing of abstract/why and concrete/how aspects relies on differential neutral substrates, which supposedly reflect the workings of partly differential cognitive substrates (e.g., Spunt et al., 2010, 2011; Spunt and Lieberman, 2012; Gilead et al., 2014). Therefore, employing a two-by-two design also allowed us to conduct a conjunction analysis which examines whether the effects of age-of-acquisition appear across different cognitive mindsets.

Study 1

Participants

Twenty-eight right-handed participants (17 females, average age 25.74, $SD = 3.08$, range 21–33 years) participated in the experiment. They were all native speakers of Hebrew, none had a history of neurological or psychiatric disorders, and all had normal or corrected-to normal vision. One participant was excluded from the final analysis due to failure to comply with task instructions. Participants gave written consent prior to taking part in the experiment. The study was approved by the Institutional Review Board of the Sourasky Medical Center, Tel-Aviv.

Materials

Out of the 50 original stimulus-pairs we selected 24 pairs that gave rise to the most marked difference in age of acquisition. The average age of acquisition for the 24 late-acquired (LA) activities was 17.74 ($SD = 2.54$) whereas that of the early-acquired activities (EA) was 4.69 ($SD = 1.72$), $t(46) = 20.81$, $p < 0.001$. The degree of social complexity, motor complexity, and positivity did not differ between the stimuli lists. There was a significant difference in the rated degree of cognitive complexity, imageability/concreteness, familiarity and frequency[1,2] (see Table 1). Each of the 24 stimulus-pairs was embedded within a question concerning mental aspects of a behavior ("why" it is performed) or physical aspects of a behavior ("how" it is performed). For example, participants answered such questions as "why do people scratch lottery tickets?" or "how do people scratch lottery tickets", resulting in a total of 96 sentences. The complete list of stimuli is provided in the open-science framework website (https://osf.io/3fegi).

Behavioral procedure

Participants were carefully instructed and trained on the task prior to entering the scanner. The training was repeated verbatim inside the scanner. The items used for the training session were taken from a different pool of sentences than the main task. Participants were instructed to silently read the questions displayed, silently generate an answer to these questions, and press a button once they finished answering.[3] Stimuli were presented with Presentation version 14.9 (Neurobehavioral Systems, CA, USA). Each question was presented on screen for 3500 ms followed by a 500 ms fixation. Participants indicated that they responded by pressing a key on a response box with their finger.

The experiment had one session lasting of 522 s. Experimental trials were intermixed with baseline trials in which a fixation cross was presented. The duration of the baseline trials randomly varied between 2 and 8 s (mean ITI = 3.45 s), totaling about one quarter of overall session duration. The sentences were randomly presented, and the order of the stimulus trials and baseline trials was determined by a sequencing algorithm designed to maximize the efficiency of the event-related design (Dale, 1999).

Finally, in order to verify the reliability of our pre-experimental stimuli ratings, we obtained participants' ratings of age-of-acquisition, familiarity, imageability/concreteness, and frequency.

Imaging procedure

Whole-brain T2*-weighted EPI functional images were acquired with a GE 3-T Signa Horizon LX 9.1 echo speed scanner (Milwaukee, WI). The experiment consisted of one scanning session in which 264 volumes were acquired (TR = 2000 ms, 200 mm FOV, 64 × 64 matrix, TE = 35, 35 pure axial slices, 3.15 × 3.15 × 3.5 mm voxel size, no gap). Slices were collected in an interleaved order. At the beginning of each scanning session, 5 additional volumes were acquired, to allow for T1 equilibration (they were not included in the analysis). Before the experiment, high-resolution anatomical images (SPGR; 1 mm sagittal slices) were obtained. Head motion was minimized by using cushions arranged around each participant's head, and by explicitly guiding the participants prior to entering the scanner. Imaging data were preprocessed and analyzed using SPM (Wellcome Department of Cognitive Neurology, London). A slice-timing correction to the first slice was performed followed by realignment of the images to the first image. Next, data were spatially normalized to an EPI template based upon the MNI305 stereotactic space. The images were then resampled

[1] Actions that are performed frequently (e.g., brushing teeth) are unlikely to be of low familiarity; however, actions that people rate as very familiar (e.g., a family dinner) could be performed relatively infrequently. In light of this, we decided to measure both familiarity and frequency.

[2] The issue of significant differences along these four dimensions was addressed in Study 2.

[3] In order to minimize motion artifacts we made use a procedure employed in a previous study (e.g., Gilead et al., 2014) in which participants did not provide overt answers to the questions, but rather responded silently. In light of this, a limitation of the current study is that we do not have a record of participants' responses on the task (other than their RT). However, past research shows (as well as the current studies) that activation pattern in the Why/How task do not differ between experiments wherein participants respond silently and experiments wherein they provide their responses during the task (e.g., see results of Spunt et al., 2010, 2011, 2016; Spunt and Lieberman, 2012 vs. Spunt and Adolphs, 2014; Spunt, et al., 2016).

Table 1
Ratings of stimuli used in Study 1. Standard deviations are shown in parentheses. Actual sample data are the ratings provided by the participants who took part in the imaging experiment. All other ratings were obtained in a pre-test.

	Late-acquired behaviors (LA)		Early-acquired behaviors (EA)		Difference (*t* value)	Difference (*p* value)
Age of acquisition	17.74	(2.54)	4.69	(1.72)	20.82	0.000000
Age of acquisition (actual sample)	17.43	(2.45)	4.97	(2.06)	19.06	0.000000
Positivity	3.38	(0.82)	3.55	(0.66)	0.82	0.415853
Social complexity	2.02	(1.12)	1.57	(0.70)	1.66	0.103501
Cognitive complexity	2.75	(0.81)	1.97	(0.70)	3.53	0.000949
Motor complexity	3.17	(0.98)	2.79	(0.82)	1.47	0.148791
Imageability/ concreteness	3.85	(0.50)	4.23	(0.46)	2.74	0.008730
Imageability (actual sample)	4.07	(0.52)	4.58	(0.32)	4.12	0.000156
Familiarity	3.38	(0.89)	4.21	(0.72)	3.54	0.000932
Familiarity (actual sample)	3.33	(0.82)	4.16	(0.61)	3.98	0.000243
Frequency	3.40	(1.05)	2.33	(0.94)	3.71	0.000561
Frequency (actual sample)	3.32	(0.93)	2.43	(0.87)	3.41	0.001362

into 2-mm cubic voxels, and finally smoothed with an 8-mm FWHM isotropic Gaussian kernel.

In order to model task-related activity in each of the relevant conditions, the canonical hemodynamic response was convolved with the onset of each trial. The general linear model was used for statistical analyses. For each subject, a fixed-effect model was implemented to linearly contrast brain activity for the effects of interest. We then computed the second-level analyses (in which subjects were treated as random effects) using one-sample *t*-tests. Significant regions of activation were identified using a threshold of $p < 10^{-4}$ with a cluster size threshold of 53 voxels, corresponding to a threshold of $p < 0.05$, corrected for multiple comparison, as assessed through Monte Carlo simulations implemented in Matlab (Slotnick et al., 2003). We ran 10,000 iterations of the simulation using the pre-defined parameters of our design, and the smoothness parameter as estimated in SPM.

Conjunction analysis was done using the stringent minimal-t statistic approach over two orthogonal contrasts (Nichols et al., 2005). The "conjunction null" was set at $p < 0.01$, two-tailed, k > 53. Monte-Carlo simulation showed that this results in a cluster-extent-corrected Family-Wise Error (FWE) rate of $p < 0.05$, two-tailed. Because the two contrasts are fully orthogonal, using these thresholds, the effective uncorrected voxel-wise probability of a false positive is $p < 10^{-4}$, k > 53. The LA conjunction analysis (LA How > EA How) ∩ (LA Why > EA Why) was implemented by running the contrast of LA How > EA How inclusively masked with the contrast of LA Why > EA Why. Similarly, the EA conjunction analysis was implemented by running the contrast of EA How > LA How inclusively masked with the contrast of EA Why > LA Why.

Results

Imaging data

Neural activity associated with processing late-acquired behaviors (LA How > EA How) ∩ (LA Why > EA Why)

In order to find the neural correlates of processing late-acquired behaviors, we searched for the conjunction of activation associated with retrieving information regarding *how* late-acquired (LA), vs. early-acquired (EA) behaviors are performed, with the activations associated with retrieving information regarding *why* late-acquired (vs. early-acquired) behaviors are performed. Processing late-acquired behaviors resulted in activation of the regions collectively referred to as the "default-mode network": the ventromedial and dorsomedial prefrontal cortex, the posterior cingulate, the left angular gyrus extending to the temporo-parietal junction, the left superior frontal gyrus, and the left middle temporal gyrus (Fig. 1 and Table 2).

In order to verify that the activation observed indeed fall within the set of neural regions collectively referred to by researchers as "the default mode network", we conducted an automated meta-analysis using Neurosynth (Yarkoni et al., 2011). We searched the Neurosynth database for studies containing the feature "default"; this search yielded 437 studies. We extracted the "reverse inference maps", which represent a comparison between all the studies in the Neurosynth database that contain the term "default" and those that do not contain this term. The resulting activation map included the ventromedial and dorsomedial prefrontal cortex, the posterior cingulate, the left angular gyrus extending to the temporo-parietal junction, the left superior frontal gyrus, the left middle temporal gyrus, and the medial-temporal lobe. All of the regions which were found to be associated with the late-acquired behaviors overlapped with the default network (Fig. 2).

Neural activity associated with processing early-acquired content (EA How > LA How) ∩ (EA Why > LA Why)

No significant clusters of activation were identified for this contrast.

LA > EA contrast

We compared the neural activity associated with retrieving information regarding late-acquired (vs. early-acquired) content irrespective of task (i.e., a main effect of age of acquisition). As noted earlier, examining the main effects of age-of-acquisition is a less controlled method of analysis as compared to the conjunction analysis, however, it yielded practically the same pattern of results as the conjunction analysis (Table 2).

EA > LA contrast

Processing early-acquired (vs. late-acquired) behaviors, irrespective of task, recruited the left inferior parietal lobule. This effect of age-of acquisition did not appear in the conjunction analysis because it was evident only within the *How* task, but not in the *Why* task.

Why > How contrast

In order to verify the reliability of our paradigm we contrasted the activity associated with thinking "why" actions are performed compared to "how" they are performed, regardless of age of acquisition. Thinking "why" was associated with activation of the medial prefrontal cortex and the posterior cingulate, which are part of the "mentalizing-network" (e.g., Van Overwalle, 2009) (Fig. 1 and Table 2). This network also consists of the superior temporal sulcus and temporo-parietal junction; these two latter regions did not survive correction for multiple comparisons, but were evident in the left hemisphere at more liberal threshold of $p < 0.005$, uncorrected. Activations in regions outside the default-mode network included several visual cortex clusters as well as a cluster in the left postcentral gyrus (see Table 2). This pattern of results closely matches previous studies which examined the same contrast (Gilead et al., 2014; Spunt et al., 2010, 2011; Spunt and Lieberman, 2012).

How > Why contrast

Thinking "how" (compared to "why") an action is performed, recruited a left-lateralized fronto-parietal network implicated in sensorimotor processing (i.e., the so-called "Mirror Neuron System"; Rizzolatti et al., 2001). Once again, this result replicates previous findings (Spunt et al., 2010, 2011; Spunt and Lieberman, 2012; Gilead et al., 2014). (Fig. 1 and Table 2).

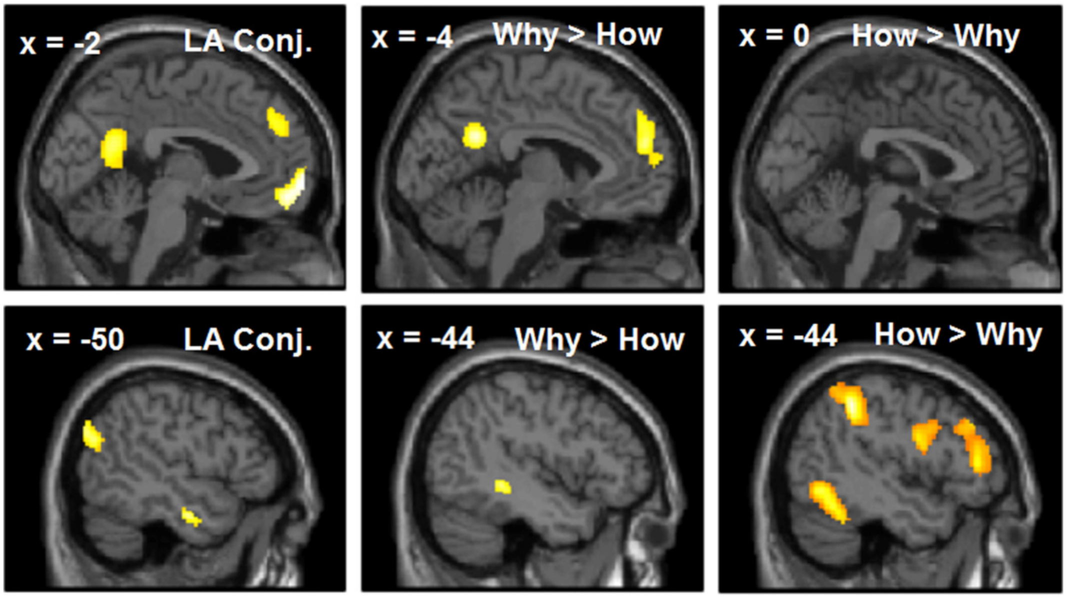

Fig. 1. Neural activity associated with task and age of acquisition. Activations are shown at a threshold of $p < 0.05$, corrected. Left: LA conjunction ((LA How > EA How) ∩ (LA Why > EA Why)); middle: Why > How; right: How > Why. Lateral views show the left hemisphere.

Behavioral results

Response times

Paired-samples *t*-tests indicated that responses times were slower for LA How ($M = 2586$ ms, $SD = 375$) than for EA How trials ($M = 2489$ ms, $SD = 346$), $t(26) = 2.73$, $p = 0.011$. There were no difference in RT for LA Why ($M = 2378$ ms, $SD = 362$) and EA Why ($M = 2328$ ms, $SD = 347$), $t(26) = 1.52$, n.s. The issue of RT differences for EA How and LA how trials was handled in Study 2 wherein stimuli were also equated in terms of frequency and imageability. A two-way analysis of variance with factors of Task (Why/How) and Age of Acquisition (LA/EA) did not reveal a significant interaction, $F(1, 26) = 1.18$, n.s. Replicating previous findings (Spunt et al., 2010, 2011; Spunt and Lieberman, 2012), the two-way analysis of variance indicated that participants took longer to

Table 2
Regions identified in the whole brain analysis in Study 1. All clusters reported here survived a cluster-extent correction for a Family-Wise Error rate of $p < 0.05$; conjunction analysis relied on the minimal t-statistic approach (i.e., testing against the "conjunction null"). [1]cluster also survives SPM's voxel-wise FWE correction; [2]cluster also survives SPM's voxel-wise FWE correction when testing against "global null" (i.e., testing whether two congruent orthogonal contrasts are consistently high and jointly significant); [3]cluster also survives cluster-extent correction irrespective of conjunction of effects (i.e., both contrasts that form the conjunction independently survived cluster-extent correction).

Contrast	Region		Coordinates			Significance level	Voxels
			x	y	z	Z-score	
(LA How > EA How) and (LA Why > EA Why)	Frontal	Dorsal medial prefrontal cortex[2,3]	−8	46	38	3.88	584
		Ventral medial prefrontal cortex[2,3]	0	60	−10	4.89	456
		L superior frontal gyrus[3]	−24	20	52	3.48	160
	Limbic	Posterior cingulate[2,3]	−6	−54	4	4.17	545
	Temporal	L temporo-parietal junction[2]	−50	−72	26	4.56	430
		L middle temporal gyrus[2,3]	−54	−6	−24	4.26	56
(EA How > LA How) and (EA Why > LA Why)	Non identified						
LA > EA	Frontal	Ventral medial prefrontal cortex[1]	−2	56	−12	5.17	1159
		L superior frontal gyrus	−26	18	52	4.21	69
	Limbic	Posterior cingulate[1]	−8	−54	6	4.99	703
	Temporal	L temporo-parietal junction	−50	−74	28	4.31	338
		L Middle temporal gyrus[1]	−50	−10	−24	5.01	110
EA > LA	Parietal	L inferior parietal lobule	−66	−36	30	4.35	80
Why > How	Frontal	Medial prefrontal cortex[1]	−8	54	26	4.82	657
		R precentral gyrus	60	−2	46	4.48	73
	Limbic	Posterior cingulate[1]	−6	−54	26	5.07	299
	Occipital	R lingual gyrus	12	−100	8	4.22	183
		L lingual gyrus	−20	−84	0	4.3	127
	Temporal	Superior temporal sulcus	−44	−36	−6	4.61	111
	Parietal	L postcentral gyrus[1]	−54	−12	54	5.27	86
How > Why	Parietal	L inferior parietal lobule[1]	−46	−42	46	6.41	3614
		R inferior parietal lobule[1]	62	−44	44	5.27	561
	Frontal	L precentral gyrus[1]	−24	4	58	5.8	963
		R middle frontal gyrus[1]	42	38	22	5.58	775
		L middle frontal gyrus[1]	−42	50	18	5.54	713
		L precentral gyrus[1]	−44	0	26	5.08	553
		R superior frontal gyrus	6	22	50	4.55	58
	Temporal	L fusiform gyrus[1]	−48	−62	−8	5.54	745
	Insular	R insula	52	14	12	4.56	237

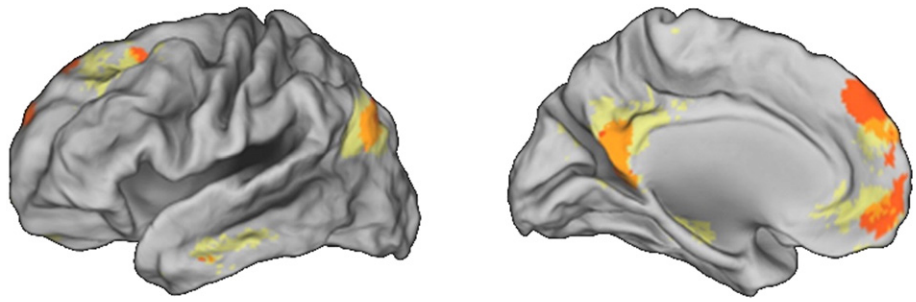

Fig. 2. The Default Mode Network. Results of an automated meta-analysis of default network activations are shown in yellow; the five clusters identified in the conjunction analysis in Study 1 are displayed in red; overlap appears in orange. All of these clusters overlapped with the default mode network.

respond to How questions ($M = 2538$ ms, $SD = 348$) than to Why questions ($M = 2442$ ms, $SD = 317$), $F(1, 26) = 9.74$, $p = 0.004$.[4]

Study 2

This study replicated Study 1 with a different set of stimuli, which were equated along all available dimensions, namely, positivity, social complexity, cognitive complexity, motor complexity, imageability, familiarity, frequency. This entailed that the age difference between late-acquired and early-acquired activities decreased from approximately 12 years in Study 1 to approximately 6 years in Study 2. Thus, in the present study the average age of acquisition for the late-acquired activities was 11.99 ($SD = 3.27$) whereas that of the early-acquired activities was 5.68 ($SD = 1.76$); importantly, this difference in age of acquisition was still highly significant, $t(46) = 8.29$, $p < 0.001$ (see Table 3; see https://osf.io/3fegi/ for a complete list of stimuli). Participants performed this experiment directly after completing Study 1.[5] Two participants that took part in the previous study did not continue to perform Study 2 due to technical issues, leaving 25 participants for the final analysis.

ROI analysis

In order to see whether activation within the six "default-network" clusters identified in Study 1 could be exclusively related to age-of acquisition, we defined them as functional regions of interest and extracted parameter estimates from each ROI on a subject-by-subject basis using MarsBaR v.042 (Brett et al., 2002). We conducted a Task (Why/How) × Age of Acquisition (LA/EA) repeated measured ANOVA on the mean beta values of each of the six ROIs. Consistent with our prior hypothesis, processing late-acquired (vs. early-acquired) activities elicited greater activity in the posterior cingulate cortex, $F(1, 24) = 11.50$, $p = 0.001$; in the angular gyrus, $F(1, 24) = 11.21$, $p = 0.001$; in the superior frontal gyrus, $F(1, 24) = 4.43$, $p = 0.022$; in the dorsomedial prefrontal cortex, $F(1, 24) = 3.44$, $p = 0.037$; and in the left middle temporal gyrus, $F(1, 24) = 4.05$, $p = 0.027$; The activity in the ventromedial prefrontal cortex displayed the same observed trend but did not attain significance, $F(1, 24) = 1.28$, n.s. None of the six regions of interest displayed a significant Task × Age of Acquisition interaction (Fig. 3).

Whole brain analysis

In order to compliment the ROI of analysis, we also performed a whole-brain conjunction analysis identical to the one performed in Study 1, i.e., (LA How > EA How) ∩ (LA Why >EA Why). The regions identified in this analysis were, once again, the posterior cingulate cortex (peak MNI coordinates: $x = -6$, $y = -58$, $z = 8$; 58 voxels), the angular gyrus ($x = -28$, $y = -84$, $z = 42$; 236 voxels) and the left superior frontal gyrus ($x = -6$, $y = 6$, $z = 64$; 66 voxels). We did not observe significant activation in dorsomedial prefrontal cortex and the left middle temporal at a threshold of $p < 0.0001$; however activation in these two regions survived a more liberal threshold of $p < 0.001$, $k = 53$. No significant activation was evident in the ventromedial prefrontal cortex.

Response times

Paired-samples t-tests did not find significant difference in responses times for LA How ($M = 2496$ ms, $SD = 374$) vs. EA How ($M = 2455$ ms, $SD = 343$), $t(24) = 1.38$, n.s., and for LA Why ($M = 2378$ ms, $SD = 362$) vs. EA Why ($M = 2328$ ms, $SD = 347$), $t(24) = 1.90$, n.s. Additionally, a two-way analysis of variance did not find an interaction of Task (Why/How) and Age of Acquisition (LA/EA), $F(1, 24) < 1$. As in Study 1, and replicating previous findings (Spunt et al., 2010, 2011; Spunt and Lieberman, 2012), a two-way analysis of variance indicated that participants took longer to respond to How questions ($M = 2475$ ms, $SD = 351$) than to Why questions ($M = 2353$ ms, $SD = 348$), $F(1, 24) = 7.16$, $p = 0.013$.

Discussion

In two studies, participants performed a semantic retrieval task wherein they processed the concrete (i.e., "how") and abstract (i.e., "why") aspects of late-acquired and early-acquired actions. Consistent with much previous research (e.g., Spunt et al., 2010, 2011; Spunt and Lieberman, 2012; Gilead et al., 2014), focusing on the abstract, why (vs. concrete, how) aspects of an action resulted in greater activation in regions collectively referred to as the "default mode network" (Raichle et al., 2001): the dmPFC, the PCC, the left TPJ, the left superior frontal gyrus, and the left middle temporal gyrus. Importantly, in accordance with our hypothesis, the activation in these regions was higher when processing later-acquired (vs. earlier acquired) actions—even when participants' goal was to focus on the concrete (i.e., "how") aspects of the action.

A plethora of neuroimaging research (e.g., Hauk et al., 2004; Tettamanti et al., 2005) has shown that people activate sensory and motor regions when they process words and sentences that describe human action (e.g., "Dana threw away the chocolate"). This evidence was taken by proponents of the "embodied cognition" framework (e.g., Barsalou, 1999; Niedenthal et al., 2005), to suggest that people's

[4] In the current study we were *not* interested in examining the neural correlates of processing Why vs. How knowledge. We report the results of the How > Why and Why > How contrast as a validation of the current paradigm in comparison to previous studies (e.g., Spunt et al., 2010, 2011; Spunt and Lieberman, 2012; Gilead et al., 2014).

[5] The fact that participants performed Study 2 after Study 1 is likely to have resulted in a training effect, as evident by shorter response latencies in Study 2. However, it is highly unlikely that an order effect would somehow interact with our variable of interest, namely, age of acquisition.

Table 3
Ratings of stimuli in Study 2. Standard deviations are shown in parenthesis. Actual sample data is the ratings provided by the participants' in the imaging experiment. All other ratings were obtained in a pre-test.

	Late-acquired behaviors (LA)		Early-acquired behaviors (EA)		Difference (t value)	Difference (p value)
Age of acquisition	11.99	(3.28)	5.69	(1.76)	8.30	0.000000
Age of acquisition (actual sample)	13.42	(3.56)	6.52	(2.01)	8.26	0.000000
Positivity	3.23	(0.70)	3.34	(0.64)	0.58	0.565053
Social complexity	1.55	(0.84)	1.61	(1.02)	0.22	0.826772
Cognitive complexity	2.16	(0.81)	2.09	(0.81)	0.31	0.761715
Motor complexity	2.56	(0.75)	2.48	(0.77)	0.37	0.711395
Imageability/concreteness	4.22	(0.37)	4.22	(0.39)	0.04	0.964475
Imageability (actual sample)	4.38	(0.43)	4.44	(0.50)	0.47	0.641543
Familiarity	3.93	(0.63)	4.08	(0.80)	0.75	0.459666
Familiarity (actual sample)	3.85	(0.68)	4.03	(0.68)	0.89	0.380302
Frequency	2.62	(0.78)	2.44	(0.99)	0.67	0.503167
Frequency (actual sample)	2.77	(0.75)	2.63	(0.91)	0.57	0.570866

ability to decipher symbolic/linguistic messages relies on a re-experiencing of concrete sensory and motor states described in the sentence. In contrast, advocates of the "classic" distinction between the perceptual and conceptual domains (e.g., Adams and Campbell, 1999) argued that it is difficult (if not impossible) to explain how the re-experiencing of tangible physical states can support the capacity of symbolic communication to convey more abstract, intangible ideas (e.g., "Dana wants to be healthy"). Recent work has offered a possible integration of these two approaches by showing that when people focus on the concrete, "how" aspects of an action, they indeed activate sensory and motor regions; however, when individuals focus on abstract, "why" aspects of the same action they rely on a network of regions involved in abstract/social cognition (Spunt and Adolphs, 2014; Spunt and Lieberman, 2012; Spunt et al., 2011; Van Overwalle and Baetens, 2009). This suggests that the degree to which people's processing of action sentences relies on concrete/embodied processing depends on participants' comprehension goals.

Our current findings are consistent with this previous work (e.g., Spunt and Adolphs, 2014; Spunt and Lieberman, 2012; Spunt et al., 2011) in showing that when participants' goal was to focus on abstract aspects of an action (e.g., the intention that is associated with it) they activated default network regions, whereas when their goal was to focus on the concrete aspects of an action they activated sensory-motor regions. We go one step further in showing that even when participants' goal is to focus on concrete/embodied forms of processing, they nevertheless may process the more abstract meanings associated with this action.

Specifically, when participants processed concrete/how aspects of actions that were acquired at a later age, at which advanced symbolic/abstract cognition was already well-developed (e.g., Inhelder and Piaget, 1958), they exhibited greater recruitment of the same regions that are involved in processing the abstract, why aspects of the action. These results support our hypothesis according to which when an action is learned at an age wherein abstract cognition is already relatively well-developed, the mental representation of the concrete aspects of this action may become mentally associated with its abstract/symbolic meanings—such that even when we think about the concrete/how aspects of this action, we will spontaneously supplement this representation with more abstract/symbolic meaning.

One important qualification is that the emergence of abstract cognition is not an all-or-none phenomenon. Whereas Piaget famously postulated the existence of a well-defined timeline for the emergence of adult cognition, modern research suggests that cognitive development may not follow clearly-defined step-wise pattern, and is characterized by much inter-individual variability (Brainerd, 1978). Additionally, some types of abstract cognition appear relatively early in development; for example, aspects of the ability to think about abstract mental states may be present in the first year of life (Cannon and Woodward, 2012; Onishi and Baillargeon, 2005). Nonetheless, Piaget's insights concerning the predominance of concrete modes of cognition in early development—and the

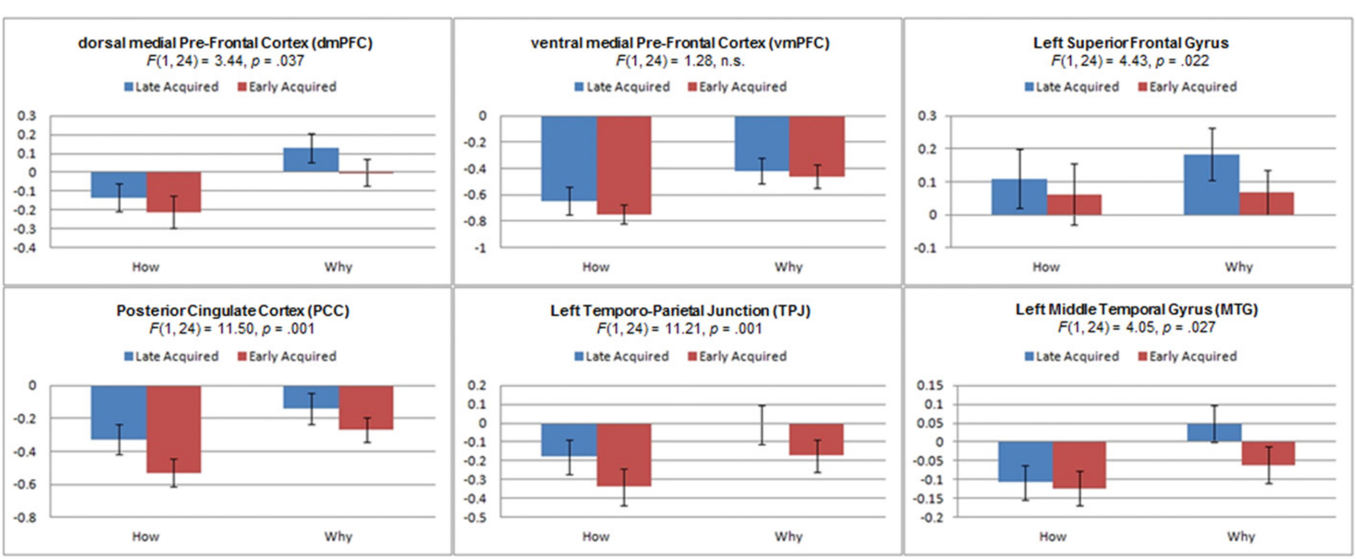

Fig. 3. Beta estimates in Study 2 showing main effect of Age of Acquisition. Regions of interest were the clusters identified in Study 1 to be associated with processing late-acquired semantic content.

gradual emergence of abstract cognition—remain highly influential, and are clearly supported by much behavioral research (e.g., Marini and Case, 1994; Ferrer et al., 2009; Susac et al., 2014; Bosco et al., 2014).

Furthermore, as noted earlier, research in developmental neuroscience has provided clear support for the presumed distinction between concrete/sensorimotor and abstract/symbolic cognition (e.g., Binder et al., 2009; Spunt et al., 2016). Whereas the neural systems that subserve sensorimotor cognition mature relatively early in ontogeny, the maturation of the neural systems involved in abstract cognition is protracted, and continues well into late adolescence (e.g., Fair et al., 2008; Supekar et al., 2010). Future research in developmental neuroscience could continue to explore how neural and cognitive development affects the neural representation of actions by applying longitudinal designs, wherein the age of acquisition of different actions will be experimentally manipulated. For example, such an experiment could entail teaching identical (novel) actions to individuals either at the age of 6 or 12, and then, later in their life, examining the neural processes that are involved in processing late- and early-acquired actions.

Our findings are consistent with recent work (Spunt et al., 2016) that showed that processing more abstract action sentences (i.e., sentences that are less readily imageable, and that describe an action that requires less physical effort) result in greater activation in default network regions. Importantly, in Study 2 of the current investigation early-acquired and late-acquired actions were equated in terms of their imageability or the degree of physicality, and yet, nonetheless, late-acquired actions resulted in greater default network activation. Thus, our results suggest that—above and beyond participants' goals when thinking of the action (i.e., focusing on why/how aspects)—*and* above and beyond the concreteness/tangibility of the action—the age of acquisition of an action also moderates default network activity.

Finally, past behavioral research suggests that people differ in the degree to which they tend to rely on more abstract vs. concrete mental representations (e.g. Vallacher and Wegner, 1989). In light of this, an interesting question for future investigation is whether such individual differences moderate the degree to which individuals spontaneously activate default network vs. sensorimotor brain regions during action processing. Such continued research may help shed light on fundamental questions concerning the development of abstract and sensorimotor cognition, as well as on the interactions between these modes of thought in adulthood.

References

Adams, F., Campbell, K., 1999. Modality and abstract concepts. Behav. Brain Sci. 22 (4), 610. http://dx.doi.org/10.1017/s0140525x99222145.

Arevalo, A.L., Baldo, J.V., Dronkers, N.F., 2012. What do brain lesions tell us about theories of embodied semantics and the human mirror neuron system? Cortex 48 (2), 242–254. http://dx.doi.org/10.1016/j.cortex.2010.06.001.

Barsalou, L.W., 1999. Perceptual symbol systems. Behav. Brain Sci. 22 (4), 577–660.

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. Cereb. Cortex 19 (12), 2767–2796. http://dx.doi.org/10.1093/cercor/bhp055.

Bosco, F.M., Gabbatore, I., Tirassa, M., 2014. A broad assessment of theory of mind in adolescence: the complexity of mindreading. Conscious. Cogn. 24, 84–97. http://dx.doi.org/10.1016/j.concog.2014.01.003.

Brainerd, C.J., 1978. Stage question in cognitive-developmental theory. Behav. Brain Sci. 1 (2), 173–181.

Brett, M., Anton, J.-L., Valabregue, R., Poline, J.-B., 2002. Region of interest analysis using the MarsBar toolbox for SPM 99. NeuroImage 16, S497.

Cannon, E.N., Woodward, A.L., 2012. Infants generate goal-based action predictions. Dev. Sci. 15 (2), 292–298. http://dx.doi.org/10.1111/j.1467-7687.2011.01127.x.

Dale, A.M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8 (2–3), 109–114. http://dx.doi.org/10.1002/(sici)1097-0193(1999)8:2/3<109::aid-hbm7>3.0.co;2-w.

de Zubicaray, G., Arciuli, J., McMahon, K., 2013. Putting an "end" to the motor cortex representations of action words. J. Cogn. Neurosci. 25 (11), 1957–1974. http://dx.doi.org/10.1162/jocn_a_00437.

Dunbar, R.I., 2004. Gossip in evolutionary perspective. Rev. Gen. Psychol. 8 (2), 100.

Fair, D.A., Cohen, A.L., Dosenbach, N.U.F., Church, J.A., Miezin, F.M., Barch, D.M., ... Schlaggar, B.L., 2008. The maturing architecture of the brain's default network. Proc. Natl. Acad. Sci. U. S. A. 105 (10), 4028–4032. http://dx.doi.org/10.1073/pnas.0800376105.

Ferrer, E., O'Hare, E.D., Bunge, S.A., 2009. Fluid reasoning and the developing brain. Front. Neurosci. 3 (1), 46–51. http://dx.doi.org/10.3389/neuro.01.003.2009.

Fodor, J.A., 1983. The Modularity of Mind: An Essay on Faculty Psychology. MIT Press.

Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. Neuron 50 (4), 531–534. http://dx.doi.org/10.1016/j.neuron.2006.05.001.

Gilead, M., Liberman, N., Maril, A., 2013a. From mind to matter: neural correlates of abstract and concrete mindsets. Soc. Cogn. Affect. Neurosci., nst031

Gilead, M., Liberman, N., Maril, A., 2013b. The language of future-thought: an fMRI study of embodiment and tense processing. NeuroImage 65, 267–279. http://dx.doi.org/10.1016/j.neuroimage.2012.09.073.

Gilead, M., Liberman, N., Maril, A., 2014. From mind to matter: neural correlates of abstract and concrete mindsets. Soc. Cogn. Affect. Neurosci. 9 (5), 638–645. http://dx.doi.org/10.1093/scan/nst031.

Hauk, O., Johnsrude, I., Pulvermüller, F., 2004. Somatotopic representation of action words in human motor and premotor cortex. Neuron 41 (2), 301–307.

Inhelder, B., Piaget, J., 1958. The Growth of Logical Thinking from Childhood to Adolescence, 1958. Kegan Paul, London.

Izura, C., Perez, M.A., Agallou, E., Wright, V.C., Marin, J., Stadthagen-Gonzalez, H., Ellis, A.W., 2011. Age/order of acquisition effects and the cumulative learning of foreign words: a word training study. J. Mem. Lang. 64 (1), 32–58. http://dx.doi.org/10.1016/j.jml.2010.09.002.

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 (7), 826–848. http://dx.doi.org/10.1016/j.cortex.2010.11.001.

Lewis, M.B., Gerhand, S., Ellis, H.D., 2001. Re-evaluating age-of-acquisition effects: are they simply cumulative-frequency effects? Cognition 78 (2), 189–205. http://dx.doi.org/10.1016/s0010-0277(00)00117-7.

Marini, Z., Case, R., 1994. The development of abstract reasoning about the physical and social world. Child Dev. 65 (1), 147–159. http://dx.doi.org/10.1111/j.1467-8624.1994.tb00741.x.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. Neuroimage 25 (3), 653–660.

Niedenthal, P.M., Barsalou, L.W., Winkielman, P., Krauth-Gruber, S., Ric, F., 2005. Embodiment in attitudes, social perception, and emotion. Personal. Soc. Psychol. Rev. 9 (3), 184–211.

Onishi, K.H., Baillargeon, R., 2005. Do 15-month-old infants understand false beliefs? Science 308 (5719), 255–258. http://dx.doi.org/10.1126/science.1107621.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. 98 (2), 676–682.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2 (9), 661–670. http://dx.doi.org/10.1038/35090060.

Schacter, D.L., Addis, D.R., Buckner, R.L., 2007. Remembering the past to imagine the future: the prospective brain. Nat. Rev. Neurosci. 8 (9), 657–661. http://dx.doi.org/10.1038/nrn2213.

Slotnick, S.D., Moo, L.R., Segal, J.B., Hart, J., 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. Cogn. Brain Res. 17 (1), 75–82. http://dx.doi.org/10.1016/s0926-6410(03)00082-x.

Spunt, R.P., Adolphs, R., 2014. Validating the why/how contrast for functional MRI studies of theory of mind. NeuroImage 99, 301–311. http://dx.doi.org/10.1016/j.neuroimage.2014.05.023.

Spunt, R.P., Lieberman, M.D., 2012. Dissociating modality-specific and supramodal neural systems for action understanding. J. Neurosci. 32 (10), 3575–3583. http://dx.doi.org/10.1523/jneurosci.5715-11.2012.

Spunt, R.P., Lieberman, M.D., 2013. The busy social brain: evidence for automaticity and control in the neural systems supporting social cognition and action understanding. Psychol. Sci. 24 (1), 80–86. http://dx.doi.org/10.1177/0956797612450884.

Spunt, R.P., Falk, E.B., Lieberman, M.D., 2010. Dissociable neural systems support retrieval of how and why action knowledge. Psychol. Sci. 21 (11), 1593–1598. http://dx.doi.org/10.1177/0956797610386618.

Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J. Cogn. Neurosci. 23 (1), 63–74. http://dx.doi.org/10.1162/jocn.2010.21446.

Spunt, R.P., Kemmerer, D., Adolphs, R., 2016. The neural basis of conceptualizing the same action at different levels of abstraction. Soc. Cogn. Affect. Neurosci. 11 (7), 1141–1151.

Stephens, G.J., Silbert, L.J., Hasson, U., 2010. Speaker–listener neural coupling underlies successful communication. Proc. Natl. Acad. Sci. 107 (32), 14425–14430.

Steyvers, M., Tenenbaum, J.B., 2005. The large-scale structure of semantic networks: statistical analyses and a model of semantic growth. Cogn. Sci. 29 (1), 41–78. http://dx.doi.org/10.1207/s15516709cog2901_3.

Supekar, K., Uddin, L.Q., Prater, K., Amin, H., Greicius, M.D., Menon, V., 2010. Development of functional and structural connectivity within the default mode network in young children. NeuroImage 52 (1), 290–301. http://dx.doi.org/10.1016/j.neuroimage.2010.04.009.

Susac, A., Bubic, A., Vrbanc, A., Planinic, M., 2014. Development of abstract mathematical reasoning: the case of algebra. Front. Hum. Neurosci. 8, 10. http://dx.doi.org/10.3389/fnhum.2014.00679.

Tettamanti, M., Buccino, G., Saccuman, M.C., Gallese, V., Danna, M., Scifo, P., ... Perani, D., 2005. Listening to action-related sentences activates fronto-parietal motor circuits. J. Cogn. Neurosci. 17 (2), 273–281.

Turner, J.E., Valentine, T., Ellis, A.W., 1998. Contrasting effects of age of acquisition and word frequency on auditory and visual lexical decision. Mem. Cogn. 26 (6), 1282–1291. http://dx.doi.org/10.3758/bf03201200.

Vallacher, R.R., Wegner, D.M., 1989. Levels of personal agency: Individual variation in action identification. J. Pers. Soc. Psychol. 57 (4), 660.

Van Hoeck, N., Ma, N., Ampe, L., Baetens, K., Vandekerckhove, M., Van Overwalle, F., 2012. Counterfactual thinking: an fMRI study on changing the past for a better future. Soc. Cogn. Affect. Neurosci., nss031
Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30 (3), 829–858. http://dx.doi.org/10.1002/hbm.20547.
Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. NeuroImage 48 (3), 564–584. http://dx.doi.org/10.1016/j.neuroimage.2009.06.009.
Watson, C.E., Cardillo, E.R., Ianni, G.R., Chatterjee, A., 2013. Action concepts in the brain: an activation likelihood estimation meta-analysis. J. Cogn. Neurosci. 25 (8), 1191–1205. http://dx.doi.org/10.1162/jocn_a_00401.
Wilson, M.A., Cuetos, F., Davies, R., Burani, C., 2013. Revisiting age-of-acquisition effects in Spanish visual word recognition: the role of item imageability. J. Exp. Psychol. Learn. Mem. Cogn. 39 (6), 1842–1859. http://dx.doi.org/10.1037/a0033090.
Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. Nat. Methods 8 (8), 665–670.