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Affordance processing in segregated parieto-frontal dorsal stream sub-pathways

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ABSTRACT

The concept of *affordances* indicates “action possibilities” as characterized by object properties the environment provides to interacting organisms. Affordances relate to both perception and action and refer to sensory-motor processes emerging from goal-directed object interaction. In contrast to stable properties, affordances may vary with environmental context. A sub-classification into *stable* and *variable* affordances was proposed in the framework of the ROSSI project (Borghi et al., 2010; Borghi and Riggio, 2015, 2009). Here, we present a coordinate-based meta-analysis of functional imaging studies on object interaction targeting consistent anatomical correlates of these different types of affordances. Our review revealed the existence of two parallel (but to some extent overlapping) functional pathways. The network for stable affordances consists of predominantly left inferior parietal and frontal cortices in the ventro-dorsal stream, whereas the network for variable affordances is localized preferentially in the dorso-dorsal stream. This is in line with the proposal of differentiated affordances: stable affordances are characterized by the knowledge of invariant object features, whereas variable affordances underlie adaptation to changing object properties.

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1. Introduction

The concept of *affordance* was introduced by the ecological psychologist Gibson (Gibson, 1979). Affordances indicate “action possibilities” as characterized by object properties the environment provides to interacting organisms. Affordances relate to perception as well as action and refer to sensory-motor processes emerging from goal-directed object interaction. For instance, the handle on a cup provides an affordance for grasping and holding it. In the traditional Gibsonian view, affordances are recorded by the perceptual system in a direct way, thus, motor responses are directly activated by objects’ affordances, independently of whether the object is recognized or not. In other words, responding to affordances does not require access to knowledge about the object. The organisms’ behavioral possibilities afforded by an object are exclusively determined by the pattern of stimulation given by the object itself.

There is, however, growing experimental evidence that affordances are not (necessarily) a static property, but can vary with changes in the environment or in the perception of an organism, arising, for instance, from visual pathologies (e.g., Young, 2006). To give a specific example, Tucker and Ellis (2004) have shown a statistically indistinguishable behavioral stimulus-response compatibility effect (i.e. faster reaction times and less error rates in the compatible than in the incompatible stimulus-response condition), obtained with both object names and object images. Hence, this effect could rather be based on memorized information than on online processing of visual information. In this context, a conceptual extension in the form of a sub-classification of affordances into *stable, variable*, and *canonical* has been proposed in cognitive psychology (Borghi et al., 2010; Borghi and Riggio, 2015, 2009). According to this, *stable affordances* emerge from slow “offline” processing of visual information based on memorized object knowledge as well as previous experiences in object interaction. They refer to invariant features or object properties incorporated into an object representation, as, for example, typical grip types. Accordingly, we *know* that a marble is graspable with a precision grip. This does not imply solely the property size as a stable affordance, but there is a greater probability that size will lead to the emergence of a stable affordance than the more variable property of the location of the marble. In contrast, *variable affordances* emerge from fast online processing of visual information during actual object interaction and refer to changing or temporary object characteristics, such as orientation in space, size changes including the update of hand shape for grasping, defining overall the *current state* of the object. Finally, *canonical affordances*, which can be considered to be associated with stable affordances, are related to canonical aspects concerning object orientation (e.g., bottles are typically experienced in an upright position). It is important to mention that object orientation could thus also lead to the emergence of stable affordances as we typically observe and interact with objects in a given orientation. We do not, therefore, consider stable and variable affordances as being strictly dichotomous but rather as being arranged along a continuum.

Visual information originates in early visual cortical areas of the occipital cortex, and is classically considered to be processed over two distinct anatomical pathways (Ungerleider and Haxby, 1994; Ungerleider and Mishkin, 1982). The ventral stream, transferring information to the inferotemporal cortex, plays an essential role in the perceptual identification of objects and in the further analysis of object characteristics, and is therefore referred to as “what” system. The dorsal stream redirects information to the posterior parietal cortex mediating the required sensorimotor transformations for visually guided object-related actions. The dorsal stream was originally referred as “where” system by Ungerleider and Mishkin (1982), who proposed the dorsal stream to be responsible for localizing objects in visual space, but was later on re-conceptualized as “how” system (Goodale and Milner, 1992). This functional scope was extended insofar as the ventral stream holds a perceptual mechanism for the identification of possible and actual goal objects from visual information as well as for the selection of an appropriate course of action to deal with those objects (vision-for-perception), whereas the dorsal stream is responsible for the online implementation of possible and actual object-related actions, as well as sustaining online action control (vision-for-action) (Goodale et al., 1994; Milner and Goodale, 1995; see Milner and Goodale, 2008, for a refinement of the terminology used within this model). To sum up, even though both streams process information about object features and spatial relations, the ventral stream focuses on the enduring characteristics of objects and their relations to form a basis for long-term perceptual representations used to identify and to recognize objects, whereas the dorsal stream uses the instantaneous and egocentric coordinates of objects to mediate the visual control of object-related actions (Goodale et al., 1994; see also Goodale and Milner, 1992).

However, a further functional-anatomical refinement in terms of dorsal sub-pathways and ventro-dorsal interactions has been intensively discussed (Derbyshire et al., 2006; Gallese et al., 1999; Jeannerod and Jacob, 2005; Pisella et al., 2006; Rizzolatti and Matelli, 2003). An important contribution –initially based on studies in non-human primates (Rizzolatti and Matelli, 2003; Rizzolatti et al., 1998)– was the proposal of two distinct “dorsal” parieto-frontal sub-pathways: a *ventro-dorsal* stream and a *dorso-dorsal* stream. The ventro-dorsal stream is formed by the middle temporal visual area MT and by the visual areas of the inferior parietal lobule and the intraparietal sulcus, such as VIP and AIP, projecting to the ventral premotor areas F4 and F5, respectively, in the frontolateral cortex–with frontal area F5 corresponding to human area 44 as the caudal part of Broca's region (see Rizzolatti et al., 1998). The dorso-dorsal stream is formed by the parieto-occipital area V6 (with afferents to this area originating in the visual areas of the occipital lobe) and areas V6a and MIP of the superior parietal lobule projecting to the dorsal premotor areas F2 and F7 in the frontal cortex. Note that original nomenclatures for non-human primate anatomical areas were included. The ventro-dorsal stream is thought to be functionally linked to object awareness for action recognition/organization, whereas the dorso-dorsal stream is proposed to subserve online control of actions (as recently discussed in detail by Binkofski and Buxbaum, 2013). Representative human data confirming the existence of two dorsal sub-pathways, as well as ventral-dorsal interactions, stem from studies on goal-directed behavior in neurologically damaged patients (e.g., Binkofski et al., 1998; Himmelbach and Karnath, 2005; Pisella et al., 2006; see also Rottschy et al., 2013).

Given the obvious parallels between the attributes of stable/variable affordances and properties of ventro-dorsal/dorso-dorsal stream, it is reasonable to hypothesize that stable affordances are processed primarily in the ventro-dorsal stream while variable affordances are supported preferably by the dorso-dorsal stream (see Fig. 1). Since stable and variable affordances are unlikely to be entirely dichotomous, a partial overlap of the respective neural correlates would also seem plausible (see Borghi and Riggio, 2015, for more details).

To investigate this further, we reviewed human brain imaging studies relevant to affordance processing. We aimed at revealing consistent anatomical correlates underlying stable and variable affordances to address potential segregation into a ventro-dorsal and a dorso-dorsal pathway. Seventy-one affordance-related studies were therefore classified independently by three expert raters. The raters categorized each study based on the experimental setting as featuring stable or variable affordances. Studies included for stable affordances did not implement a change in the active or observed action plan, as e.g. in reach-to-grasp actions toward constant objects, whereas variable affordances were employed in studies in which the action plan of an active or observed action changed due to a change of one or more object characteristics, as e.g. grasping of objects with different length or judgment concerning the graspability of objects with different length or in different orientations.

This implies that experimental settings involving stable or variable affordances can employ tasks on actual object interaction and/or mere observation of object interaction and thus indicates a relationship to the perception-action matching system or mirror neuron system (MNS). Mirror neurons have been initially discovered as a class of neurons in the monkey area F5 "that become active when the *monkey acts* on an object *and* when the *monkey observes another monkey or the experimenter* making goal-directed actions" (Rizzolatti and Fadiga, 1998; see Gallese et al., 1996; Rizzolatti et al., 1996; see also Rizzolatti and Craighero, 2004, for a review on the characteristics of the MNS in humans). The human MNS has been defined as the cortical circuit matching observed, meaningful actions onto the observer's motor system, thereby facilitating recognition and imitation (for an overview see Buccino et al., 2004; Rizzolatti, 2005). Premotor neurons in adjacent monkey area F4 were also reported to code spatial properties of an object in motor terms, i.e., motor properties related to dynamically changing velocity (Fogassi et al., 1996). It is therefore reasonable to assume a common ground of action observation and actual performance–at least for transitive actions. Beyond that, in our view, the mere observation of an object –as for instance in a *stable* object recognition task or a *variable* mental object rotation task– activates the simulation of possible interactions, mediated through the canonical neuron system. This system consists of grasping neurons that are also activated by the mere presentation of visual objects, even when grasping movements are explicitly excluded, as initially found in area F5 of the non-human primate brain by Murata et al. (1997); (see also Rizzolatti and Fadiga, 1998).

2. Meta-analysis methods

2.1. Literature search and categorization criteria

We conducted an exhaustive literature search including functional magnetic resonance imaging studies on object interaction in healthy humans indexed in the Ovid MEDLINE database. Our proceeding comprised following steps:

(1) We searched for individual predefined search terms in both title and abstract fields. Each search used the function Map Term to Subject Heading (MeSH). In detail, the following keywords or phrases were used as search terms: affordance*, grasp*, precision grip, power grip, reach*, point*, imagined grasp*, imagined reach*, imagined point*, object* size, object* shape, object* weight, object* orientation, object* location, object* rotation, mental rotation, object* recognition, imitation, object* action, tool-use, visuo-motor, mirror neuron*, parietal, fMRI. These search terms were used to find studies on affordances in general, though some terms already indicate stable versus variable experimental settings, as e.g. grasp* and object* orientation respectively (see constrains for categorization below and in Table 1, for detailed definitions and task examples). Note that we used an asterisk to indicate a truncation of a given search term in order to increase search results. For example, grasp* enabled us to find words such as e.g., grasping, grasped, or grasp-related in both title and abstract fields.

(2) Searches for individual terms (excepting the last three) were combined using the OR function (i.e., retrieving records containing any of the defined search terms). Separately, we also linked the concepts "mirror neuron*" and "parietal" with the OR function and subsequently combined both search results using the AND function (i.e., retrieving records containing all defined search terms). Finally, these results were narrowed by combining with the concept "fMRI", also using the AND function.

(3) We limited results to studies investigating humans and published in English since 1995. The described search was conducted on September 09th 2014, but we continued to include papers matching the criteria provided by the Ovid MEDLINE AutoAlert function until May 31th 2015.

(4) The 469 studies thus identified were manually screened for further limitations. Specifically, we excluded studies on patients, children, and solely left-handed participants, as well as studies using non-fMRI imaging techniques, that did not report activation maxima in standard space (i.e., coordinate system by Talairach or the Montreal Neurological Institute (MNI)), or provide whole brain contrasts. To ensure consistent experimental conditions and stimuli to the largest degree possible, we further excluded studies not showing 3-dimensional or concrete reachable/graspable objects. Studies not showing real or realistic-looking objects were also excluded.

The search yielded 71 studies, which were categorized independently by three raters familiar with the concept of affordances, as featuring stable, variable, or mixed affordances. The latter category could be used in the exceptional case of uncertainty in classification or rather when aspects of both stable and variable affordances were implemented in the experimental task. Categorization was based

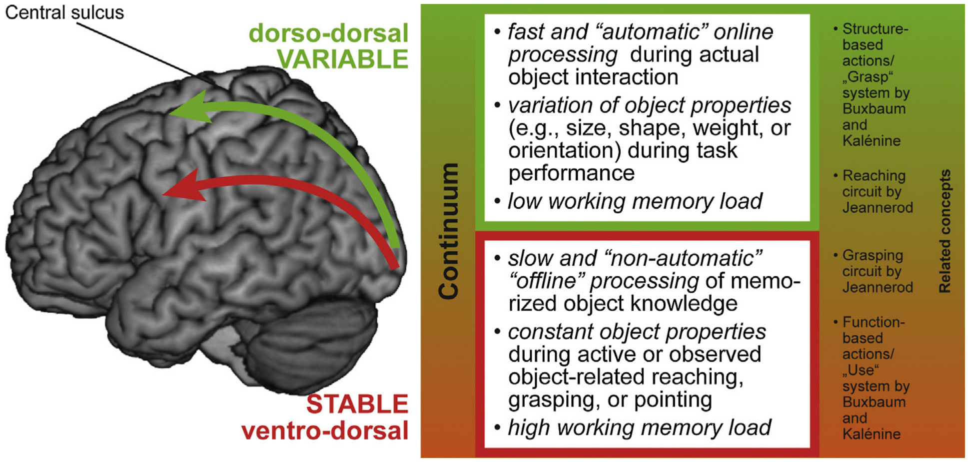

Fig. 1. Conceptual illustration. Schematic relative location of the ventro-dorsal and the dorso-dorsal processing pathway in relation to our proposed dissociation of stable and variable affordances and their further characteristics to related concepts.

Table 1
Constrains for categorization of stable and variable affordances. Summarized definition criteria related to study and task examples. Note that the definition of the respective task as passive, i.e., pure perceptual [P], or active, i.e., involving action execution [A] are indicated in brackets.

Definition criteria	Study example	Task example
Stable affordances		
Active or observed *reaching, grasping, or pointing with one or more objects that did not change their properties* during task performance, or objects with constant size, shape, or weight	Cavina-Pratesi et al., 2007	Grasping versus reaching toward one of two objects [A]
	Pierno et al., 2009	Observation of static images representing the hand of a human model pointing to or grasping of an object [P]
Grasping with different object-related grip types	Begliomini et al., 2007	Precision/whole hand grasping versus reaching [A]
Action observation using either photographs or video clips of *someone else reaching towards and grasping, or pointing to objects*	Hamzei et al., 2012	Action observation by use of videos of a hand grasping objects [P]
Active or observed *pantomime of object-directed motor acts*	Hermsdörfer et al., 2007	Execution of pantomimed and actual tool use [A] Observation and preparation of pantomimed and actual tool use [P]
Object recognition requiring a judgment on motor relevant properties of an object or a tool	Grèzes et al., 2003b	Object recognition task requiring power/precision grip to (task-irrelevant) congruent/incongruent object-size [A]
	Hattori et al., 2009	Object recognition task requiring a judgment about graspability [P]
Variable affordances		
Variations of the same object in size, shape, weight, or orientation during task performance (i.e., from trial-to-trail)	Simon et al., 2002	Pantomimed grasping of object stimuli of different outline shapes appearing in different orientations [A]
	Ehrsson et al., 2007	Grip force adjustment to unexpected changes of weight [P]
Object recognition including different perspectives of an object	Sugio et al., 1999	Canonical versus non-canonical object orientation views in a passive observation task [P]
Mental object rotation of real or realistic-looking object stimuli	Vingerhoets et al., 2002	Mental rotation task: same-different judgment about pairs of hands and tools [P]

on the studies' experimental settings and the following constraints (see Borghi et al., 2010; Borghi and Riggio, 2015, 2009; see also Table 1 for a summary and task examples): Experiments selected for *stable* affordances used reaching, grasping, or pointing tasks employing one or more objects that did not change their properties during task performance, or, more precisely, objects with constant size, shape, or weight. We included studies using active or observed pantomime of object-directed motor acts, as well as action observation tasks using either photographs or video clips of someone else reaching towards and grasping, or pointing to objects. Grasping tasks were included if the task required different object-related grip types to be executed or observed. Object recognition tasks were considered relevant if subjects had to make a judgment on motor relevant properties of an object or a tool. This implicated canonical affordances as being coded as *stable* affordances. Experiments selected for *variable* affordances included variations of the same object in size, shape, weight, or orientation during task performance (i.e., from trial-to-trail). Importantly, merely presenting objects at different locations was not a sufficient reason for classification into the variable category if the affordance itself remained stable. To give an example, showing an object with an afforded handle on the right side (e.g., a coffee mug) at different locations on a table characterizes a stable affordance, since the canonical orientation (considered to be associated with stable affordances) remains constant. But showing this coffee mug in rotated views, i.e., with changes of the handle orientation, refers to a variable affordance. We thus included studies using different perspectives of an object (in particular non-canonical object orientation) to the variable category, along with mental object rotation tasks using real or realistic-looking object stimuli. To sum up, the *stable* affordance category thus includes experimental settings in which the active or observed action does not include a spontaneous or planned change of the action plan. The *variable* affordance category on the other hand includes active or observed actions that require a spontaneous or planned change of the action plan because of a change of one or more object characteristics.

An inter-rater reliability analysis using the Kappa statistic was performed to determine consistency among raters. The Randolph's free-marginal multi-rater kappa value was found to be 0.634, with 75.6% overall agreement using the Online Kappa Calculator (http://

justusrandolph.net/kappa/; see Randolph, 2005; Warrens, 2010), indicating substantial agreement between the three raters (see Landis and Koch, 1977). However, inter-rater reliability might vary between raters depending on expert knowledge of the affordances concept as shown by the single Kappa values (rater1 versus rater2: Kappa = 0.524, rater1 versus rater3: Kappa = 0.648, rater2 versus rater3: Kappa = 0.411).

The final assignment of a study was based on a unique majority vote among the three raters. Here, we coded 1, 2, or 3 as referring the study to the stable, variable, or mixed category respectively. For instance, all studies evaluated as 2-1-2, 1-2-2, or 2-2-3 were assigned to the variable category. Overall, the meta-analysis identified 44 studies on stable affordances and 27 studies on variable affordances. A detailed overview of each study, including the categorization by the three raters, the paradigm/task employed in the respective study as well as the reported contrasts is given in Table 2 for the stable category and in Table 3 for the variable category. Note that our classification of contrasts in direct task contrasts and baseline contrasts including both control task contrasts and rest contrasts is not definite in every case and might differ from the definition made by the authors according to their experimental questions.

2.2. *Meta-analysis algorithm and procedure*

In contrast with narrative reviews or label-based anatomical approaches, coordinate-based meta-analysis methods aggregate statistically activation foci (‘peaks’) derived from neuroimaging data in order to emphasize specific neuronal patterns across multiple studies following a common paradigm or hypothesis (Eickhoff et al., 2012, 2009; Goodkind et al., 2015; Rottschy et al., 2012).

For the present meta-analysis, we used the revised Activation Likelihood Estimation (ALE) algorithm for coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009; Laird et al., 2009; Turkeltaub et al., 2012), implemented using in-house MATLAB tools. This algorithm identifies areas showing a topographic convergence of reported coordinates across experiments higher than those expected under a random spatial association. The key idea behind ALE is to treat the reported foci not as single points, but rather as centers for three-dimensional Gaussian probability distributions, capturing the spatial uncertainty associated with each focus. The probabilities of all foci reported in a given experiment were then combined for each voxel, resulting in a modeled activation map (Turkeltaub et al., 2012). Taking the union across these modeled activation maps yielded voxel-wise ALE scores describing the convergence of results at each particular location in the brain. To distinguish ‘true’ convergence between studies from random convergence (i.e., noise), ALE scores were compared to an empirical null-distribution (Eickhoff et al., 2012) reflecting a random spatial association between experiments. Hereby, a random-effects inference is invoked, focusing on inference on the above-chance convergence between studies, not clustering of foci within a particular study. The p-value for a “true” ALE was then given by the proportion of equal or higher values obtained under a null-distribution of random spatial association between experiments. The resulting non-parametric p-values for each meta-analysis were then thresholded at a cluster-level family-wise error corrected threshold of $p < 0.05$ (cluster-forming threshold at voxel-level $p < 0.001$) and transformed into Z-scores for display.

The relation of meta-analyses was revealed by difference and conjunction analyses. Thereby, differences between conditions were tested by first performing separate ALE analyses for each condition and computing the voxel-wise difference between the ensuing ALE maps (Eickhoff et al., 2011). All experiments contributing to either analysis were then pooled and randomly divided into two groups with the same size as the two original sets of experiments reflecting the contrasted ALE analyses. ALE-scores for these two randomly assembled groups were calculated and the difference between these ALE-scores was recorded for each voxel in the brain. Repeating this process 10,000 times then yielded an expected distribution of ALE-score differences under the assumption of exchangeability. The “true” difference in ALE scores was then tested against this null-distribution, yielding a posterior probability that the true difference was not due to random noise in an exchangeable set of labels, based on the proportion of lower differences in the random exchange. The resulting probability values were thresholded at $p > 0.95$ (95% chance for true difference) and masked inclusively by the respective main effects, i.e., the significant effects of the ALE analysis for the particular condition. Conjunction analyses aimed at identifying the intersection between the meta-analyses on both processing stable and variable affordances. That is, only regions significant on the cluster-level family-wise error corrected level in both individual analyses were considered.

The resulting areas were anatomically labeled by reference to probabilistic cytoarchitectonic maps of the human brain using the SPM Toolbox v1.8 (Eickhoff et al., 2007, 2005). Activations were assigned to the most probable histological area at their respective locations by using a Maximum Probability Map. Details on these cytoarchitectonic regions may be found in the following publications reporting on superior parietal cortex (Area SPL (7A)/Area SPL (7PC): Scheperjans et al., 2008a, 2008b), inferior parietal cortex (Area IPC (PFt)/Area IPC (PF)/Area IPC (PFcm): Caspers et al., 2008, 2006), intraparietal sulcus (Area hIP3: Scheperjans et al., 2008a, 2008b), Broca’s region (Area 44 and Area 45: Amunts et al., 1999), premotor cortex (Area 6: Geyer, 2004), primary somatosensory cortex (Area 2: Grefkes et al., 2001; Area 3a and Area 1: Geyer et al., 1999, 2000), visual cortex (Area hOC5 (V5): Malikovic et al., 2007), and cerebellum (Lobule VI (Hem): Diedrichsen et al., 2009).

3. Meta-analysis results

First, we calculated the main meta-analyses for both processing stable and variable affordances, as well as a conjunction analysis. To increase the statistical power of the main meta-analyses, we included all types of contrasts –i.e., direct task contrasts as well as both “high level” and “low level” baseline contrasts. Affordance-related brain activation can be obtained from all types of contrasting brain activation. Direct task contrasts reveal defined “relative” activations associated with an experimental condition in relation to another experimental condition in a given task (e.g., observation of grasping > observation of touching), while baseline contrasts reveal absolute activations associated with a given task by contrasting an experimental task against a control task (e.g., observation of grasping > observation of a still image), which is referred to as “high level” baseline contrast, or by contrasting an experimental task against fixation/relaxing periods (e.g., observation of grasping > rest periods), which is referred to as “low level” baseline contrast. This does not implicate that we included all reported contrasts of a study in any case, even though in most studies we indeed regarded all reported contrasts as affordance-related, and excluded only reported deactivations obtained by contrasting a baseline task with the affordance-related task as e.g., judgment about scrambled pictures (used as control task baseline) > judgment about object grasping (Buxbaum et al., 2006).

Based on both main meta-analyses for the processing of stable and variable affordances respectively, we calculated difference analyses by directly comparing STABLE > VARIABLE and VARIABLE > STABLE (see Fig. 2 and Table 4) to identify distinct activations for stable versus variable affordances. Additionally, we disentan-

Table 2
Summary of publications entered into the main meta-analysis for stable affordances, including categorization by the four raters, the paradigm/task employed in the respective study as well as the reported contrasts.

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampelsize
Begliomini et al., 2007	1-2-1 > stable	Action execution: Precision/whole hand grasping versus reaching	(D) Precision grip > reaching	6	12
			(D) Whole hand grip > reaching	3	
			(D) Precision grip > whole hand grip	1	
Biagi et al., 2010	1-3-1 > stable	Perceptual: Observation of complex and simple object-manipulation tasks executed with the left and the right hand	(B) All hand action observation > static initial frame	22	12
Buccino et al., 2001	1-1-1 > stable	Perceptual: Object-related action observation	(B) Object-related mouth actions > static face	9	12
			(B) Object-related arm/hand actions > static hand	6	
			(B) Object-related foot actions > static foot	4	
Buxbaum et al., 2006	1-1-1 > stable	Perceptual: Judgments about object grasping and functional use	(B) Grasp > scrambled pictures	3	15
			(B) Non-prehensile use > scrambled pictures	2	
			(B) Prehensile use > scrambled pictures	5	
			(D) Non-prehensile use > prehensile use	4	
			(D) Non-prehensile use > grasp	1	
Cavina-Pratesi et al., 2007	1-3-1 > stable	Action execution: Grasping versus reaching toward one of two objects	(D) Grasping > reaching	8	9
		Perceptual: Size versus pattern discrimination between two objects	(D) Size > pattern	4	
Choi et al., 2001	1-1-1 > stable	Action execution: Pantomiming tool-use gestures	(B) Pantomine > oppositional finger tapping	15	10
Chong et al., 2008	1-2-1 > stable	Perceptual: Observation of moving and stationary images of reach-to-grasp hand actions, while performing an attentionally demanding task	(B) Observation of moving hand and type of grip discrimination (functional localizer)	14	15
Chouinard et al., 2009	2-1-1 > stable	Perceptual + Action execution: Size-weight illusion task	(R) Object lifting > rest	10	12
			(D) Adaptation to size: different > same	5	
			(D) Adaptation to weight: different > same	1	
			(D) Effects of density: different > same	1	
			(D) Effects of density: same > different	3	
			(D) Effects of false perception of weight: same weight illusion > same size–same weight	1	
			(D) Effects of false perception of weight: same weight illusion > same size–same weight ∩ effect of density	1	
Culham et al., 2003	1-2-1 > stable	Perceptual: Object perception localizer	(B) Object perception localizer	5	7
		Action execution: Visually guided grasping versus reaching towards objects	(D) Grasping > reaching	11	
Di Dio et al., 2013; Experiment 1	2-1-1 > stable	Perceptual: Observation of reaching movements	(B) Arm > control still image	17	14
			(B) Cylinder > control still image	3	
Fabbri et al., 2014	1-2-1 > stable	Action execution: Center-out reach-to-grasp/touch task performed in five reach directions	(R) All movement types > baseline collapsed across reach direction, baseline refers to all periods not explicitly modeled	10	16
Fridman et al., 2006	1-1-1 > stable	Perceptual: Preparation of instructed-delay transitive and intransitive hand gestures	(R) Planning-preparation of transitive gestures	11	19
		Action execution: Execution of instructed-delay transitive and intransitive hand gestures	(R) Execution of transitive gestures	5	
		Perceptual	(D) Planning-preparation of transitive gestures > intransitive gestures	3	
		Action execution	(D) Execution of transitive gestures > intransitive gesture	7	

Table 2 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampelsize
Gallivan et al., 2011b	1-2-1 > stable	Perceptual + Action execution: Delayed movement towards a single object: grasp top/bottom versus reach to touch	(B) Activity elicited by the planning of a hand action (i.e., after movement instruction) versus the transient activity elicited by visual presentation of the object before the instruction: plan > preview	17	8
Gallivan et al., 2013	1-1-1 > stable	Action execution: Planned and executed grasp or reach actions with either their left or right hand toward a single target object	(D) Execute (GraspL + GraspR + ReachL + ReachR) > Preview (GraspL + GraspR + ReachL + ReachR)	24	11
Grèzes et al., 2003a	1-1-1 > stable	Perceptual + Action execution: Observation of an object/observation of an object being grasped and execution of appropriate grasp for the shown object/imitation of the shown grasping movement	(B) Conjunction analyses for observation and execution: object observation > stationary background ∩ object appropriate grasp > power grip	1	12
			(B) Conjunction analyses for observation and execution: observation of object being grasped > stationary background ∩ active imitation of grasping movement > power grip	7	
Grèzes et al., 2003b	1-1-1 > stable	Action execution: Object recognition task requiring power/precision grip to (task-irrelevant) congruent/incon-gruent object-size	(D) Regression analysis between the parameter estimates of the main effect congruency and the difference in reaction times between congruent and incongruent trials	5	12
Hamzei et al., 2003	1-1-1 > stable	Perceptual: Action recognition task	(B) Observation of grasping movement performance by different persons (ACTIVE) > passive viewing of the same actors (PASSIVE) to control for visual input	3	12
Hamzei et al., 2012	1-1-1 > stable	Perceptual: Action observation of hand grasping objects and imitation in fine motor grasping tasks	(D) Interaction action observation: AO RH, mirror training group > control training group	15	26
Hattori et al., 2009	1-1-1 > stable	Perceptual: Object recognition task requiring a judgment about graspability	(R) Conjunction analysis: graspable objects > rest ∩ nongraspable objects > rest	67	17
			(D) Graspable objects > nongraspable objects	2	
			(D) Contrasts between different functional categories	7	
			(D) Psychophysiological interaction from the regions of interest in the inferior parietal lobe within the contrast graspable objects > nongraspable objects	5	
Hermsdörfer et al., 2007	1-1-1 > stable	Perceptual: Actual and pantomimed tool use Action execution: Actual and pantomimed tool use	(R) Pantomimed tool use observation (event 1) > rest	17	23
			(R) Pantomimed tool use preparation (event 2) > rest	17	
			(R) Pantomimed tool use execution (event 3) > rest	30	
			(D) Actual tool use > rest pantomine tool use in event 1	2	
			(D) Actual tool use > rest pantomine tool use in event 2	3	
			(D) Actual tool use > rest pantomine tool use in event 3	37	
Hoeren et al., 2013	1-1-1 > stable	Perceptual: Action observation of tool-associated movements involving semantic knowledge	(D) SemanticsIncorrect > SemanticsCorrect	8	29
			(D) HandIncorrect > HandCorrect	2	
Johnson-Frey et al., 2003	1-1-1 > stable	Perceptual: Observation of static pictures of the same objects (familiar tools or unfamiliar three-dimensional shapes) being grasped or touched while performing a 1-back orienting task	(D) Observation of grasping > observation of touching	9	17
Johnson-Frey et al., 2005	1-1-1 > stable	Perceptual + Action execution: Planning versus executing object-related gestures (tool use) in a go-nogo paradigm	(B) Right hand (Experiment 1): preparation of tool use gestures > preparation of non-meaningful movements	26	13 (Exp. 1)
			(D) Right hand (Experiment 1): execution of tool use gestures > preparation of tool use gestures	7	

Table 2 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampel size
			(B) Left hand (Experiment 2): preparation of tool use gestures > preparation of non-meaningful movements	13	11 (Exp. 2)
			(D) Left hand (Experiment 2): execution of tool use gestures > preparation of tool use gestures	13	
			(B) Centroids of clusters activated during gesture planning (preparation of tool use gestures, preparation of non-meaningful movements) for both the right (Experiment 1) and left (Experiment2) hand	15	24(Exp. 1 + 2)
Mecklinger et al., 2004; Experiment 3	1-1-1 > stable	Perceptual: Object recognition and visual working memory task: comparison of movement features or sizes of two subsequently presented objects	(B) Movement > baseline task	3	10
			(B) Size > baseline task	2	
			(D) Movement > size	7	
			(D) Size > movement	5	
Menz et al., 2009	1-1-1 > stable	Perceptual + Action execution: Imitation of abstract gestures and object-related actions	(R) Independent component analysis: action perception > rest	5	15
			(R) Independent component analysis: motor preparation and action execution > rest	15	
			(R) Independent component analysis: encoding and retrieval into and from motor working memory > rest	10	
			(R) Independent component analysis: dynamic integration of object affordances > rest	9	
Molenberghs et al., 2010	1-1-1 > stable	Perceptual + Action execution: (1) passive observation (2) imitation of pantomimed goal-directed hand-actions (3) execution of an action in response to a word cue (4) self-selected execution of an action	(D) Conjunction analysis: observation ∩ imitation ∩ self-selected execution ∩ word-cued execution	6	20
Molinari et al., 2013	1-1-1 > stable	Perceptual: Observation of either reaching/grasping hand actions or matching static pictures	(R) Move > base(rest)	3	16
			(D) Move > static	3	
			(R) Static > base(rest)	4	
Morrison et al., 2013	1-1-1 > stable	Perceptual: Action observation of hand-object interaction	(D) Painful graps > all	12	14
			(D) Main effect of action (grasp > withdraw)	6	
			(D) Main effect of action (withdraw > grasp)	2	
			(D) Main effect of object (noxious > neutral)	11	
			(D) Interaction of object and action (appropriate > inapproriate action)	11	
Ocampo et al., 2011	1-2-1 > stable	Action execution: Reach-to-grasp similar and dissimilar action execution within imitative and complementary action context	(D) Interaction context (imitative/complementary) by control stimulus (observation of hand actions/symbolic arrow cue stimuli)	2	12
			(D) Main effect context (imitative > complementary)	2	
Oliver and Thompson-Schill, 2003	3-1-1 > stable	Perceptual: Binary decision about shape, color and size of auditory presented object names	(B) Shape retrieval > auditory lexical decision (word-nonword)	20	7
			(B) Size retrieval > auditory lexical decicion (word-nonword)	12	
			(B) Color decision > auditory lexical decision (word-nonword)	8	
Oosterhof et al., 2012	1-2-1 > stable	Perceptual + Action execution: Cup-shaped object interaction: manipulation with eyes open (execution) versus eyes closed (imagery)	(R) Perform + imagery > rest baseline	20	12
Peeters et al., 2009; Experiments 1–4	1-1-1 > stable	Perceptual: Observation of human or mechanical hand grasping objects (Experiment 1)	(B) Observation of human hand actions > static pictures	20	20
			(D) Interaction between the factor type of action (biological versus artificial) and the factor type of condition (action versus control static pictures)	13	
		Perceptual: Observation of human hand grasping or simple tool pick up objects (Experiment 2)	(D) Interaction between the factor type of action (biological versus artificial) and the factor type of condition (action versus control static pictures)	8	21

Table 2 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampelsize
		Perceptual: Observation of human hand grasping or simple tool pick up objects (Experiments 3 + 4)	(D) Conjunction of tool versus hand action interactions	3	16
Péran et al., 2010	1-1-1 > stable	Perceptual + Action execution: Semantic representation of action verbs and mental representation of actions	(R) Overt verb generation of action performed with depicted object (GenA) activation > rest control	10	12
			(R) Mental simulation of action (MSoA) activation > rest control	9	
			(R) Overt mime of action (MimA) activation > rest control	12	
			(R) Conjunction analysis: GenA ∩ MSoA ∩ MimA	9	
			(B) Overt verb generation of action performed with depicted object (GenA) > overt object naming (ON)	4	
			(B) Mental simulation of action (MSoA) > overt object naming (ON)	2	
			(D) Mental simulation of action (MSoA) > overt verb generation of action performed with depicted object (GenA)	8	
			(D) Overt verb generation of action performed with depicted object (GenA) > mental simulation of action (MSoA)	6	
Pierno et al., 2006	1-1-1 > stable	Perceptual: Observation of a human model reaching towards and grasping a three-dimensional target object in isolation or alongside a distractor object	(B) Main effect of type of observed behavior: reach-to-grasp action > static scene	13	14
			(D) Interaction between type of observed behavior and distractor: (reach-to-grasp action with distractor > static scene with distractor) > (reach-to-grasp action without distractor > static scene without distractor)	4	
Pierno et al., 2009	1-1-1 > stable	Perceptual: Observation of static images representing the hand of a human model pointing to or grasping of an object	(B) Conjunction analysis: pointing to an object ∩ grasping an object ∩ control (resting in proximity of an object)	11	15
			(B) Pointing to an object > resting in proximity of an object	4	
			(B) Grasping an object > resting in proximity of an object	8	
			(D) Grasping an object > pointing to an object	5	
Renzi et al., 2013	1-1-2 > stable	Action execution: execution of reach-to-grasp movements	(D) Sensory feedback (between subjects factor)	1	15
			(D) Interaction sensory feedback by object distance (within subjects factor)	4	
Shmuelof and Zohary, 2006	1-3-1 > stable	Perceptual: Observation of object manipulation by a right or left acting hand in the right or left visual field	(B) Observation of object manipulation > visual control (spatially scrambled video clip)	15	14
			(D) Hand-activity-related activation (observation of contralateral acting hand > observation of ipsilateral acting hand)	2	
Turella et al., 2009	1-1-1 > stable	Perceptual: Observation and execution of reach-to-grasping action	(B) Main effect of type of observed task: (model grasping + hand alone grasping) > (model static + hand alone static)	16	17
			(D) Main effect of type of view: (model grasping + model static) > (hand grasping + hand static)	3	
			(D) Main effect of type of view: (hand grasping + hand static) > (model grasping + model static)	1	
		Action execution	(B) Grasping execution > object fixation	4	
Valyear et al., 2012	1-1-2 > stable	Perceptual + Action execution: Observation of either the same (repeated) tool or a different (non-repeated) tool followed by grasping and demonstrating how to use a specific tool	(R) Main effect of task (tool identity/color) versus rest: congruent trials involved repeated tool identity/color (TR/CR) + incongruent trials involved changed tool identity/color (TC/CC)	6	11

Table 2 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampelsize
			(D) Main effect of congruency: congruent trials involved repeated tool identity/color (TR/CR) > incongruent trials involved changed tool identity/color (TC/CC)	3	
			(D) Interaction task by congruency	1	
Vingerhoets et al., 2011	1-1-1 > stable	Perceptual + Action execution: Planning and execution of pantomimes of equally graspable familiar and unfamiliar tools	(B) Planning the pantomime of familiar tools > planning of nontool related goal-directed transitive movements	11	16
			(B) Executing the pantomime of familiar tools > execution of nontool related goal-directed transitive movements	8	
			(B) Planning the pantomime of unfamiliar tools > planning of nontool related goal-directed transitive movements	5	
			(B) Executing the pantomime of unfamiliar tools > execution of nontool related goal-directed transitive movements	8	
			(D) Conjunction analysis: Conjunction analysis: executing > planning the pantomime of familiar tools controlled for nontool transitive movements: (FamToolexec > FamToolplan) ∩ (Controlexec > Controlplan)	16	
			(D) Conjunction analysis: executing > planning the pantomime of unfamiliar tools controlled for nontool transitive movements: (UnfamToolexec > UnfamToolplan) ∩ (Controlexec > Controlplan)	16	
Vingerhoets et al., 2012	1-1-1 > stable	Perceptual: Observation of natural transitive hand tool grasping actions	(B) Conjunction analysis of left and right hand first-person perspective relative to control condition: (FP/RH > ContrR) ∩ (FP/LH > ContrL)	21	12
			(B) Conjunction analysis of left and right hand third-person perspective relative to control condition: (TP/RH > ContrR) ∩ (TP/LH > ContrL)	17	
Vingerhoets et al., 2013	1-1-1 > stable	Perceptual: Decision on hand posture matching the functional use of shown tool object	(B) Conjunction analysis of each experimental condition versus control condition: (match > control) ∩ (mismatch easy > control) ∩ (mismatch hard > control)	7	17
			(D) Mismatch hard > mismatch easy	1	
			(D) Within > between grasp type choice	1	
Wadsworth and Kana, 2011	1-1-1 > stable	Perceptual: Observation and imagination of tool use	(R) Viewing tools > fixation	10	32
			(R) Imagined tool use > fixation	9	
Yoon et al., 2012	1-1-1 > stable	Perceptual: Observation of pantomime of congruent or incongruent actions performed	(D) Main effect task: object > action	2	17
			(D) Main effect task: action > object	7	
			(D) Main effect stimulus: congruent > incongruent	7	
			(D) Main effect stimulus: incongruent > congruent	2	
			(D) Task by stimulus interaction: action, congruent > incongruent & object, incongruent < congruent	4	
			(D) Task by stimulus interaction: object, congruent > incongruent & action, incongruent > congruent	6	

Note: Raters categorization codes were: 1 = stable, 2 = variable, 3 = mixed (stable + variable). Abbreviations: N = Number of, (D) = direct contrast between affordance-related conditions, (B) = baseline contrast contrasting an affordance-related task against a control task, (R) = baseline contrast contrasting an affordance-related task against rest.

Table 3
Summary of publications entered into the main meta-analysis for variable affordances, including categorization by the four raters, the paradigm/task employed in the respective study as well as the reported contrasts.

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampel size
Braadbaart et al., 2013	2-2-1 > variable	Perceptual + Action execution: Imitation or observation of actions involving the movement of a handle	(B) Move > watch > rest	10	16
Chapman et al., 2002	2-2-1 > variable	Action execution: Reach-to-grasp movement towards target balls	(D) Three-stimuli > one-stimulus/one-location	6	9
			(D) Three-stimuli > one-stimulus/three-possible-locations	2	
			(D) One-stimulus/three-possible-locations > one-stimulus/one-location	3	
Creem-Regehr and Lee, 2005	2-3-2 > variable	Perceptual: Viewing/imagine grasping images of tools with handles or objects with neutral graspable shapes	(B) Viewing tools > scrambled tool images	10	12
			(B) Viewing shapes > scrambled shape images	1	
			(D) Viewing tool > viewing shape	1	
			(B) Imagine grasping tools > scrambled tool images	15	
			(B) Imagine grasping shapes > scrambled shape images	13	
			(D) Imagine grasping tools > imagine grasping shapes	5	
Ehrsson et al., 2007	2-2-2 > variable	Perceptual: Grip force adjustment to unexpected changes of weight	(B) Upload of weight > static grip and rest period	5	6
			(B) Unload of weight > static grip and rest period	13	
			(D) Upload > unload	3	
			(D) Unload > upload	1	
Faillenot et al., 2001	2-2-2 > variable	Perceptual: Orientation identification of 2D objects and gratings with regard to a reference or orientation discrimination of pair differences	(B) Orientation identification > dimming detection	20	6
			(B) Orientation discrimination > dimming detection	24	
			(D) Orientation identification > orientation discrimination	5	
			(D) Object orientation identification/discrimination > grating orientation identification/discrimination ∩ general network for orientation identification/discrimination	3	
Filimon et al., 2007	2-2-2 > variable	Action execution: Reaching to pictures of abstract shapes	(B) execution of reaching > passive viewing	35	15
		Perceptual: Observation of reaching to pictures of abstract shapes	(B) observation of reaching > passive viewing	14	
		Perceptual: Imagery of reaching to pictures of abstract shapes	(B) imagery of reaching > passive viewing	13	
Gallivan et al., 2011a	2-2-2 > variable	Perceptual + Action execution: Passive viewing of objects at reachable versus unreachable locations accessible by either the left hand, right hand, or neither hand including reaching and grasping the same objects	(D) nearR > nearL + farR + farL	4	13
Hirose et al., 2010	2-2-2 > variable	Perceptual: Object recognition task requiring a judgment about graspability of objects of various sizes or about size comparison	(B) Motor evaluation > baseline task	6	17
			(B) Size comparison > baseline task	9	
James et al., 2002; Experiments 2 and 3	2-3-2 > variable	Perceptual: Observation of repeatedly presented objects from different viewpoints	(B) Intact object > scrambled object images (Experiment 2)	4	14 (8 in Exp. 2 and 6 in Exp. 3)
			(B) Intact object > scrambled object images (Experiment 3)	4	
Jenmalm et al., 2006	2-2-2 > variable	Perceptual + Action execution: Lifting objects of different weight	(B) Main effect of unexpected change in object weight: change to heavier/to lighter > no change heavy/light	1	12
			(D) Interaction−differences between heavier and lighter than predicted: (change to heavier > no change heavy) > (change to lighter > no change light) and (change to lighter > no change light) > (change to heavier > no change heavy)	4	

Table 3 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Sampelsize
Johnson et al., 2002	1-2-2 > variable	Perceptual: Jugdement on graspability	(B) Hand preparation for movement simulation–trials on which subjects were shown a meaningless precue (double-headed arrow) followed by the broken handle were subtracted from average responses from trials	58	8
			(D) Grip selection–average BOLD responses from trials on which subjects were precued to prepare either the left or right hand, but then were shown a broken, ungraspable handle were subtracted from mean responses on trials where they prepared either hand and then selected the most natural grip for engaging an unbroken dowel	20	
Jordan et al., 2001	2-2-2 > variable	Perceptual: Mental rotation task: same-different judgment about pairs of rotated three-dimensional objects	(R) Mental rotation of objects > rest	6	9
			(R) Mental rotation of abstract figures > rest	7	
			(R) Mental rotation of letters > rest	5	
			(B) Mental rotation of objects > baseline tasks	2	
			(B) Mental rotation of abstract figures > baseline tasks	4	
			(B) Mental rotation of letters > baseline tasks	2	
			(B) Mental rotation of objects + abstract figures + letters > baseline tasks	2	
Keehner et al., 2006	2-2-2 > variable	Perceptual: Imagination of transformations of objects (mental rotation) and the self (perspective taking)	(B) Mental rotation > control 0°	6	14
			(D) Mental rotation > perspective taking	4	
Króliczak et al., 2007	2-2-1 > variable	Action execution: Real or pantomimed grasping versus reaching towards objects with varying length or in an adjacent location without a present object	(D) Real grasping > real reaching	12	10
			(D) Pantomimed grasping > pantomimed reaching	12	
			(D) Pantomimed movement > real movement	2	
Malfait et al., 2010	2-2-2 > variable	Perceptual: Observation of reaching movements in human and robot	(B) reach observation > scrambled movies	12	14
Milner et al., 2006	2-2-2 > variable	Perceptual + Action execution: Rigid versus flexible object manipulation in stable and highly unstable states without vision	(R) Holding a flexible object in a stable equilibrium position (stable) > resting baseline	1	19
			(R) Balancing a rigid object at an unstable equilibrium position (unstable-r) > resting baseline	3	
			(R) Balancing the flexible object at an unstable equilibrium position (unstable-f) > resting baseline	4	
			(D) Unstable-r > stable	1	
			(D) Unstable-f > stable	4	
			(D) Unstable-f > unstable-r	2	
Mosier et al., 2011	2-1-2 > variable	Action execution: Control of four objects with increasing instabilities but requiring constant strength	(B) Sustained compression > rest (relaxed but stable grip)	17	15
			(B) Cyclic compression > rest (relaxed but stable grip)	15	
			(D) Task by dexterity interaction	4	
Nocchi et al., 2012	2-2-2 > variable	Perceptual: Observation and retrieval of upper limb and abstract object movements used in robotic training	(B) Arm movement (AM) > dot trajectory (DT)	1	22
			(B) Target point following AM (AMT) > target point following DT(DTT)	1	
			(D) Congruent target point following AM (AMCT) > incongruent target point following AM (AMIT)	4	
Ogawa and Inui, 2012	2-2-2 > variable	Perceptual: Imitation-matching task: judgment on correct imitation regarding action goal, means of manipulation, effector used, and movement trajectory	(D) Conjunction analysis: (CUP > GRASP) ∩ (CUP > HAND) ∩ (CUP > PATH)	12	23

Table 3 (*Continued*)

Publication	Raters and final categorization	Paradigm/Task	Contrast	Nfoci	Samplesize
			(D) Conjunction analysis: (GRASP > CUP) ∩ (GRASP > HAND) ∩ (GRASP > PATH)	1	
			(D) Conjunction analysis: (HAND > CUP) ∩ (HAND > GRASP) ∩ (HAND > PATH)	9	
			(D) Conjunction analysis: (PATH > CUP) ∩ (PATH > GRASP) ∩ (PATH > HAND)	4	
Schubotz et al., 2012	2-1-2 > variable	Perceptual: Multi-object every day actions versus tai chi movements	(D) boundary-detection related activity specific for action (as in contrast to tai chi movements): interaction (ACT-BO > TAI-BO) > (ACT-NOBO > TAI-NOBO)	5	17
			(R) Conjunction analysis: (ACT > null) ∩ (TAI > null) ∩ (ACT-Cloud > null) ∩ (TAI-Cloud > null)	12	
Shmuelof and Zohary, 2005	2-2-3 > variable	Perceptual: Observation of object manipulation in video clips	(D) right hand/left object > left hand/right object	13	11
			(D) count interacting finger (action-oriented) > naming the object (object-oriented)	6	
Simon et al., 2002	2-2-2 > variable	Action execution: Pantomimed grasping of an object (different outline shapes appearing in different orientations and different colors)	(B) Visually guided pantomimed hand-grasping movement > mentally name of object color	16	10
			(D) Grasping task (grasping task > pointing task, grasping task > calculation task, grasping task > saccades task, grasping task > attention task, grasping task > language task)	6	
Sugio et al., 1999	2-2-1 > variable	Perceptual: Object recognition in canonical versus non-canonical views in a passive observation task	(D) Non-canonical viewing condition > canonical viewing condition	7	12
Terhune et al., 2005	2-2-1 > variable	Perceptual: Object recognition in canonical versus non-canonical views in a covert naming task	(D) Non-canonical viewing condition > canonical viewing condition	8	8
Vanrie et al., 2002	2-2-2 > variable	Perceptual: Viewpoint-dependency (mental rotation) versus viewpoint-independency in three-dimensional block figures	(B) Invariance > control (same–different judgment task using two-dimensional T-shaped stimuli)	6	6
			(B) Rotation > control (same–different judgment task using two-dimensional T-shaped stimuli)	8	
			(D) Invariance > rotation	5	
			(D) Rotation > invariance	6	
Vingerhoets et al., 2002	2-2-2 > variable	Perceptual: Mental rotation task: same-different judgment about pairs of hands and tools	(B) Rotated hands > non-rotated hands	6	12
			(B) Rotated tools > non-rotated tools	9	
			(D) Rotated hands > rotated tools	3	
			(D) Rotated tools > rotated hands	3	
Zacks et al., 2003	2-2-2 > variable	Perceptual: Imagination of an array of objects rotating (object-based transformation) versus imagination of themselves rotating around the array (perspective transformation)	(D) main effect of transformation	3	16

Note: Raters categorization codes were: 1 = stable, 2 = variable, 3 = mixed (stable + variable). *Abbreviations*: N=Number of, (D) = direct contrast between affordance-related conditions, (B) = baseline contrast contrasting an affordance-related task against a control task, (R) = baseline contrast contrasting an affordance-related task against rest.

gled these effects for visual perception tasks and visual action tasks separately (see Appendix, including Fig. A1 and Table A1).

3.1. *Main effect for processing stable affordances*

The main meta-analysis for the processing of stable affordances (based on 129 experiments; 668 unique subjects; average of 15 subjects per experiment) showed stronger left-hemispheric and confluent fronto-parietal activations as compared to the right hemisphere. In detail, the first large left-hemispheric activation cluster comprised dorsal precentral gyrus (Area 6) and dorsal postcentral gyrus (Area 2) extending to both superior and inferior parietal lobule (SPL (7A) and IPC (PFt)), while the second large left-hemispheric activation cluster encompassed ventral precentral gyrus and pars opercularis of inferior frontal gyrus (Area 44). The right-hemispheric activation pattern involved precentral gyrus, dorsal postcentral gyrus (Area 2) extending to superior parietal lobule (SPL (7PC)), and parieto-temporal foci (IPC (PF)). In addition the middle temporal gyrus was activated bilaterally.

3.2. *Main effect for processing variable affordances*

The main meta-analysis for the processing of variable affordances (based on 76 experiments; 340 unique subjects; average of 12.4 subjects per experiment) yielded bilateral, dorsally located fronto-parietal activations covering superior parietal lobule (Area SPL (7A)), supplementary motor area (Area 6), and dorsal precentral gyrus/middle frontal gyrus. Two smaller activation clusters were located in right middle temporal gyrus and left inferior parietal lobule (IPC (PF)).

3.3. *Conjunction and contrast analyses*

Intersecting activations of both main meta-analyses for stable and variable affordances as revealed by the conjunction analysis STABLE ∩ VARIABLE comprised left superior parietal lobule (SPL (7PC)) extending to superior frontal gyrus (Area 6) and right dorsal postcentral gyrus (Area 2). Smaller conjunctive activation clusters were found in right middle temporal gyrus as well as right middle frontal gyrus. To identify distinct activations for stable versus variable affordances, we calculated difference analyses (see bottom panel in Fig. 2). The direct contrast STABLE > VARIABLE yielded an activation pattern comprising predominantly of left inferior parietal and frontal cortices. Specifically, left inferior parietal lobule (IPC (PFt)), bilateral ventral and left dorsal precentral gyrus (Area 6), left pars triangularis of inferior frontal gyrus (Area 45), as well as left middle temporal gyrus, were found to be activated more strongly for stable affordances. In contrast, more dorsally located parietal areas and right dorsal precentral gyrus were found to be activated by the opposing direct contrast VARIABLE > STABLE.

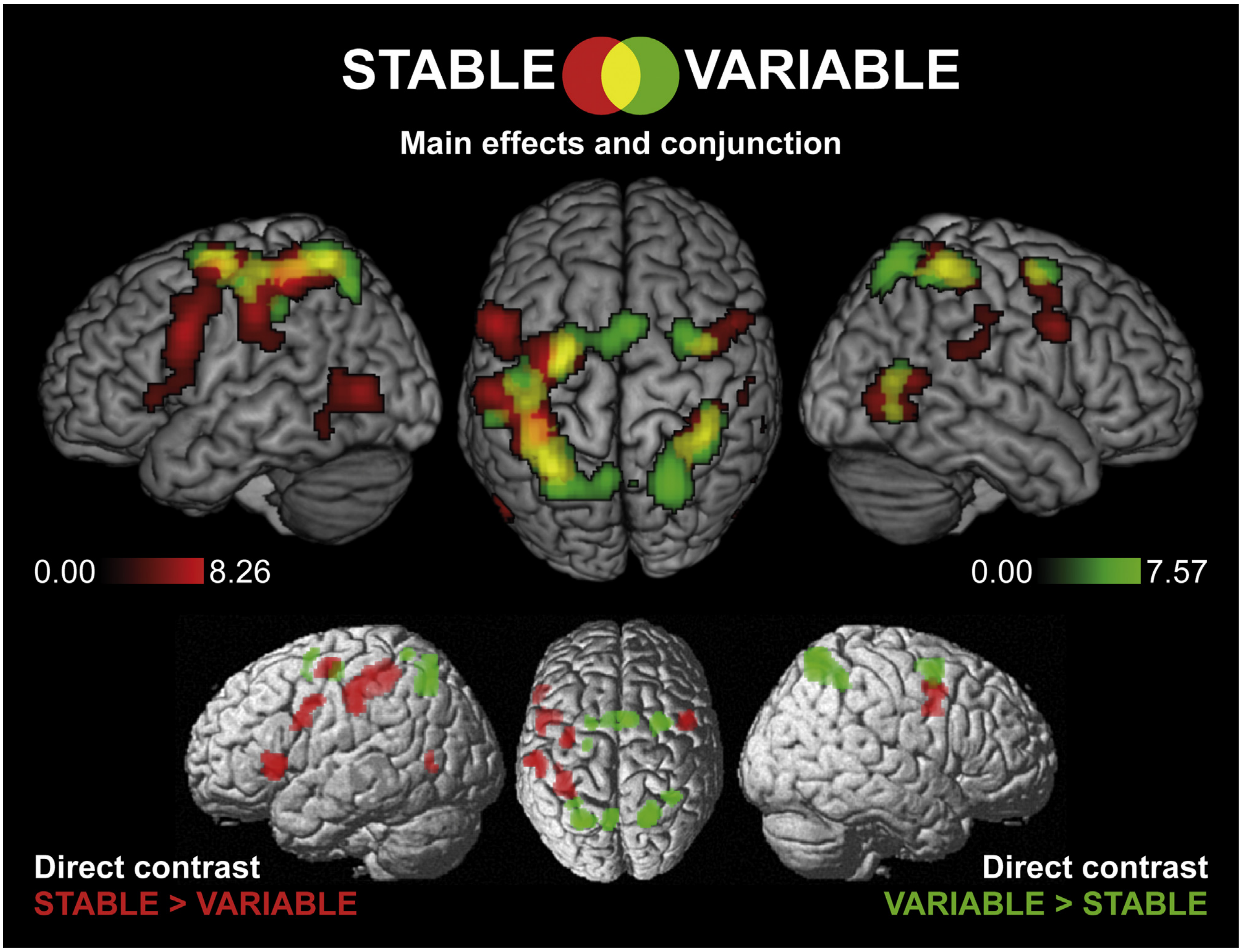

Fig. 2. Main effect of both stable affordances (red) and variable affordances (green), and conjunctive activations (yellow) shown above, as well as differences as revealed by the direct contrasts stable affordances versus variable affordances shown below. The statistical images were thresholded at $p < 0.05$, FWE corrected for the cluster level, superimposed on left, top, and right views of the volume rendered MNI template using the software MRIcron Version 06/2013 (http://www.nitrc.org/projects/mricron/).

Table 4

Macroanatomical structure, cytoarchitectonic area ($\text{Area}_{\text{cyto}}$), percent overlap of cluster with cytoarchitectonic area, cluster size in voxel, MNI coordinates (x, y, z), and maximum T value (T_{max}) of the local maxima from both main effect of stable affordances and main effect of variable affordances, the conjunction analysis, and the direct contrasts stable affordances versus variable affordances. The significance level was set to $p < 0.05$, FWE-corrected for the cluster level. Abbreviations: L. = left, R. = right.

Local maximum in macroanatomical structure	$\text{Area}_{\text{cyto}}$	Percent overlap of cluster with cytoarchitectonic area	Cluster size (voxel)	MNI coordinates			T_{max}
				x	y	z	
Main effect STABLE							
L. Postcentral Gyrus	Area 2	22.1	3346	−38	−38	54	8.29
L. Precentral Gyrus[a]	Area 6	13.2		−30	−8	60	7.83
L. Inferior Parietal Lobule[a]	IPC (PFt)	7.5		−56	−24	38	6.57
L. Superior Parietal Lobule[a]	SPL (7A)	8.7		−30	−58	60	6.38
L. Precentral Gyrus			1096	−54	6	30	7.10
L. Inferior Frontal Gyrus (Pars opercularis)[a]	Area 44	42.1		−48	6	28	6.73
R. Postcentral Gyrus	Area 2	58.4	627	36	−40	56	6.12
R. Superior Parietal Lobule[a]	SPL (7PC)	10.0		30	−52	56	4.27
L. Middle Occipital Gyrus	hOC5 (V5)	9.4	581	−44	−70	4	6.07
L. Middle Temporal Gyrus[a]				−44	−60	10	4.51
R. Precentral Gyrus			550	46	6	32	5.87
R. Middle Temporal Gyrus			546	56	−58	8	5.38
R. Cerebellum	Lobule VI (Hem)	78.4	129	22	−50	−22	5.58
R. Superior Temporal Gyrus	IPC (PF)	31.7	128	62	−36	20	3.92
R. SupraMarginal Gyrus[a]	IPC (PFcm)	24.0		60	−28	24	3.84
Main effect VARIABLE							
L. Superior Parietal Lobule			1856	−28	−64	48	7.60
L. Superior Parietal Lobule[a]	SPL (7A)	42.5		−30	−56	64	6.63
R. Superior Parietal Lobule	SPL (7A)	28.5	1472	22	−64	60	6.67
R. Supplementary Motor Area (SMA)	Area 6	17.9	1007	6	6	56	6.63
L. Precentral Gyrus[a]	Area 6	51.3		−26	−12	60	6.52
R. Middle Frontal Gyrus			353	30	9	54	5.68
R. Middle Temporal Gyrus			177	48	−64	10	4.59
L. Inferior Parietal Lobule	IPC (PF)	67.2	107	−56	−36	40	4.53
Conjunction STABLE ∩ VARIABLE							
L. Superior Parietal Lobule	SPL (7PC)	13.2	858	−30	−58	62	6.06
L. Superior Parietal Lobule[a]	SPL (7A)	27.0		−34	−50	62	5.41
R. Postcentral Gyrus	Area 2	59.2	418	38	−42	60	5.34
L. Superior Frontal Gyrus	Area 6	52.2	305	−26	−10	60	6.28
R. Middle Temporal Gyrus	hOC5 (V5)	32.9	130	48	−66	8	4.30
R. Middle Frontal Gyrus			103	38	−2	54	4.51
Direct contrast STABLE > VARIABLE							
L. Inferior Parietal Lobule	IPC (PF)	6.9	239	−58	−24	44	3.09
L. Inferior Parietal Lobule[a]	IPC (PFt)	35.1		−54	−24	34	2.74
L. Precentral Gyrus	Area 6	13.9	166	−54	0	38	3.60
R. Precentral Gyrus			164[b]	46	0	38	3.26
L. Inferior Frontal Gyrus (Pars triangularis)	Area 45	51.6	134	−54	24	−2	3.80
L. Precentral Gyrus	Area 6	57.5	95	−36	−10	60	2.78
L. Middle Temporal Gyrus			42	−46	−64	4	2.44
Direct contrast VARIABLE > STABLE							
L. Inferior Parietal Lobule	Area 2	70.9	238	−38	−40	52	2.38
R. Precentral Gyrus			164[b]	48	2	44	3.45

[a] Note that for some activation clusters we report more than the first maxima. Sub-maxima are indicated by an asterisk.

[b] Indicates one cluster with two sub-maxima.

4. Discussion

The present meta-analysis reviewed the consistent anatomical basis for processing different types of affordances. We began by discussing a refinement and extension of the Gibsonian affordance-concept (Gibson, 1979) that resulted in the proposal of a sub-classification of affordances into stable and variable ones (Borghi et al., 2010; Borghi and Riggio, 2015, 2009; see also a comment by Pellicano et al., 2011, for the idea of affordance adaptability embedded in the context of grounded cognition). This new conceptualization built upon the notion of "micro-affordances" (potentiated elements of an action, see Ellis and Tucker, 2000), representing the product of conjoint visuo-motor brain activation (Tucker and Ellis, 2004, 1998), and focused on context and flexibility (Borghi et al., 2012; Costantini et al., 2011; Natraj et al., 2013; Pellicano et al., 2010; Tipper et al., 2006). Hence, this concept provides a theoretical framework for a more flexible explanation of processes emerging in the interaction with objects.

4.1. Functional-anatomical conceptualization

The hypothesis for our meta-analysis was inspired by obvious parallels between the attributes of stable and variable affordances, and the properties of the newly proposed dorsal sub-pathways, namely the ventro-dorsal and dorso-dorsal stream (Pisella et al., 2006; Rizzolatti and Matelli, 2003). Specifically, the ventro-dorsal stream is assumed to rely on memorized knowledge and thus to operate in a slower "offline" mode as compared to the dorso-dorsal stream (Borghi and Riggio, 2009), while the dorso-dorsal stream is the most direct and immediate pathway for visual information processing and thus supports an online mode of fast visuo-motor transformation, like an "automatic pilot" (Pisella et al., 2000;

Rossetti et al., 2005). Even if the ventro-dorsal stream operates more slowly than the dorso-dorsal stream, it is by no means static: different types of neurons in the anterior intraparietal area in non-human primates –assumed to be part of the ventro-dorsal pathway– were shown to interact dynamically during different information processing stages involved in executing a hand manipulation task; i.e., they appear also to be involved in fast action planning processes (Sakaguchi et al., 2010). Therefore, the anterior intraparietal area could represent an interface of the ventro-dorsal and the dorso-dorsal stream. The evidence on timing (slower versus faster activation depending on the involved stream) is related to the processes involving the two different streams, the faster operating dorso-dorsal and the slower operating ventro-dorsal stream. However, to the best of our knowledge the only available experimental evidence on different timing of affordances activation was obtained by Jax and Buxbaum (2010), who demonstrated the existence of a competition between slower but longer-lasting "use" responses and rapid but short lasting "grasp" responses to conflict objects, i.e., objects that evoke different kinds of grips. So far, there is no evidence for different timing of activation for different kinds of affordances–i.e., stable and variable. However, due to the fact that affordances activate different systems –i.e., ventro-dorsal versus dorso-dorsal– and are involved in different –i.e., off-line versus online– processes, we can hypothesize that stable and variable affordances operate in a slower and faster mode, respectively. Beyond this, we consider the ventro-dorsal stream to hold high working memory load, whereas the dorso-dorsal stream very likely features low working memory capacity. The ventro-dorsal stream therefore operates slower as compared to the dorso-dorsal stream, but can process more and even more complex information (see Fig. 1).

Our meta-analytic review revealed that stable affordances are processed preferentially in a left-hemispheric network comprising inferior parietal and frontal cortices, whereas variable affordances were found to be processed in a bilateral network located dorsally relative to the former one. Both networks overlap pronouncedly in dorsal parieto-frontal areas. These findings confirm that stable and variable affordances are indeed processed in distinct, although overlapping, parallel parieto-frontal sub-pathways: the ventro-dorsal stream and the dorso-dorsal stream respectively. As expected, stable affordances tend to be processed mostly in the ventro-dorsal stream, while variable affordances tend to be processed more in the dorso-dorsal stream. The overlapping areas, as revealed by the conjunction analysis, reflect brain regions that are generally involved in information processing in object interaction. These areas may represent convergence zones for an exchange of information between both streams. Alternatively, our definition of a dissociating affordance concept as not being strictly dichotomous but rather as being arranged along a continuum may basically justify the overlapping activations. Despite the differential rating results, 29 out of the 44 "stable" studies and 16 out of the 27 "variable" studies were unanimously rated. This was more than half of the respective studies finally categorized as featuring stable or variable affordances. Conjunctive activations are localized mainly along the intraparietal sulcus and the superior frontal sulcus. We hypothesize that the areas along the intraparietal sulcus sample and converge information from the inferior parietal lobule and the superior parietal lobule and process synthetic information for object-oriented action. Areas around the superior frontal sulcus merge information from the ventrolateral premotor cortex and the dorsolateral premotor cortex to process the final action plans for object-oriented actions. This may indicate a close interchange of information between the intraparietal sulcus and the superior frontal sulcus.

In particular, the anterior intraparietal cortex as the human functional homologue of the macaque anterior intraparietal area –located near the junction of the anterior intraparietal sulcus and the postcentral sulcus– seems to play an integrative role for sensorimotor information (Verhagen et al., 2012; see also Binkofski et al., 2007), although perceptual and spatial features of an object are assumed to be analyzed in two anatomically distinct neural pathways. Given the supposed key role of the anterior intraparietal cortex in visuo-motor transformations involved in grasping and object manipulation (Frey et al., 2005), its causal contribution was demonstrated using the "virtual lesion technique": transcranial magnetic stimulation applied during online adjustment of grasping (Tunik et al., 2005; Verhagen et al., 2012).

4.2. Parallels to clinical data and clinical relevance

The outlined functional-anatomical dissociation within the dorsal pathway is also in line with clinical data obtained from patients affected by stroke with neurological damage (for an overview see Binkofski and Buxbaum, 2013; see also Daprati and Sirigu, 2006). The major functional role of the dorso-dorsal stream is online control of actions, thus, the cardinal deficit associated with a lesion in the dorso-dorsal stream –usually comprising the superior parietal lobule, the intraparietal sulcus and the parieto-occipital sulcus (Karnath and Perenin, 2005; Perenin and Vighetto, 1988)– is optic ataxia, characterized by misreaching towards objects during visually guided reaching (see Bálint, 1909; Borchers et al., 2013; Garcin et al., 1967). Indeed, the lack of online motor control in patients with optic ataxia, as demonstrated for reaching (Khan et al., 2005; Pisella et al., 2000; Rossetti et al., 2005) and also grasping (Milner et al., 2001; Prablanc et al., 2003), highlights the specificity of the superior parietal cortex and the parieto-occipital junction for goal-directed visuo-motor transformations involving short-lived processes. In contrast, the ventro-dorsal stream is thought to underlie more advanced processing of sensorimotor information. A lesion in the ventro-dorsal stream involving the occipito-temporal cortex and inferior parietal cortex typically causes limb apraxia, characterized by impairments at the cognitive rather than the pure motor level (Buxbaum et al., 2005; Haaland et al., 1980; Pisella et al., 2006 see also Bolognini et al., 2015). Both imitation and pantomime of object use, as well as real object interactions, are affected by limb apraxia (see Martin et al., 2015, for ventro-dorsal stream lesion-symptom mapping of different aspects of tool use in a large sample of acute stroke patients). Given that optic ataxia is regarded as a typical disorder of the dorso-dorsal stream, on-line motor performance is preserved in most cases of limb apraxia (Hoeren et al., 2014; Pisella et al., 2006; see also Ambron et al., 2015, for an interesting case report of a patient presenting with both symptoms).

The types of apraxia differentially affect the activities of daily life. Accordingly, there are differences in the prognosis of recovery and the required physiotherapeutic treatment. Therefore, a detailed knowledge about the relation of lesion localization and syndrome characterization is of great relevance for clinical practice (Binkofski and Fink, 2005). Patients with optic ataxia as an isolated visuo-motor disorder or as a symptom of the Balint's syndrome show difficulties in reorientation in an unfamiliar environment due to problems in realigning gaze to target objects to grasp by fixation. The rehabilitation program for patients showing the optic ataxia symptom should include visuo-perceptual retraining to improve visual scanning (see Toyokura and Koike, 2006; for a comprehensive case report). Impaired imitation in limb apraxia patients can hamper motor learning in physiotherapeutic treatment. The restricted ability to compensate for the impairment in indication of target-objects or actions by pantomime is even worse for patients who suffer additionally from aphasia. Therefore, limb apraxia treatment focuses on gesture training (see Smania et al., 2006, for the evidence of persistency of positive effect of the intervention), apart from strategy training or the direct training of the activities of daily living (see Dovern et al., 2012; for a review and guideline for diagnostics and treatment; see also Cantagallo et al., 2012).

It is certainly the case that the clinical relevance of affordance processing or rather the affected affordance perception and interaction with objects is not restricted to stroke patients, but may be also obvious –though neglected in research– in the psychiatric syndrome of addiction. Interestingly, Klinke and Jónsdóttir (2014) related the smoking experience to the concept of affordances to analyze how smoking affects action possibilities in patients with chronic obstructive pulmonary disease. The authors argued that "the person addicted to smoking is almost automatically drawn to smoking affordances in the environment and creates opportunities for continued smoking without conscious thought". Health care professionals should therefore be guided by the exploration of smoking affordances and how they are perceived by the individual.

4.3. *Related concepts*

Several related but not consistently overlapping concepts have been discussed prior or in parallel to our proposal of dissociative affordances in relation to different anatomical pathways and may also overlap with each other. It is worth highlighting the "Two Action Systems" (2AS) proposing a differentiation between function- and structure-based actions or the "use" and the "grasp" system (Buxbaum and Kalénine, 2010; see also Binkofski and Buxbaum, 2013, and Daprati and Sirigu, 2006; see Fig. 1), as well as the separation of a reaching circuit from a grasping circuit (see Jeannerod et al., 1995, and also Fig. 1). These concepts originated, however, from behavioral data obtained from healthy persons and patients after stroke–in contrast to the foregrounded anatomical linkage in our proposal.

Both the similarities and the differences of the 2AS with our distinction between stable and variable affordances have been discussed in detail by Borghi and Riggio (2015). Similarly, both action systems are supposed to be mediated by different processing pathways. The function-based action system or "use" system comprises of left-lateralized superior temporal and inferior parietal areas of the ventro-dorsal stream, and is concerned with more stable conceptual knowledge of an action, such as the typical features characterizing a reach-to-grasp action, regardless of the specific object to be grasped and of the kind of grip which is used. The structure-based action system or "grasp" system involves dorsolateral fronto-parietal areas of the dorso-dorsal stream bilaterally, and is functionally specialized for continuously updated visual information processing related to object shape, size, and location, and thus enables object interaction. Both action systems are not independent but highly interactive, as reflected by the time course of activation. Accordingly, objects might evoke both function- and structure-based response actions at the same time that interfere with each other (see evidence by Bub et al., 2008). As already mentioned, Jax and Buxbaum (2010) demonstrated a competition between slower but longer-lasting function-based "use" responses and rapid but short lasting structure-based "grip" responses to objects evoking different kinds of grips. Thus, the obvious similarity between our stable-variable dissociation and the proposal by Buxbaum and Kalénine (2010) lies in the observation that an object incorporating affordances is to be associated with processing of information differing in content and time course, i.e., long term information such as that characterizing stable affordances, and online information such as that characterizing variable affordances. In our view, stable affordances, however, are not necessarily dedicated to functional information in object-related actions. Stable affordances concern the typical way in which we grasp and manipulate objects such as cherries, apples, or nails. However, when considering the distinction between structure-based grip –as e.g., grasping a marble– and functional grip specific to skilled use –as e.g., the grip used to manipulate with a screwdriver– (see e.g., Boronat et al., 2005; Canessa et al., 2008; Watson and Buxbaum, 2015), a potential sub-specification of stable affordances might be reasonable. Since we do not consider stable and variable affordances to be strictly dichotomous, but rather arranged along a continuum, the relation of the function-based "use" system and the structure-based "grasp" system to stable and variable affordances, respectively, is likewise characterized by a continuous transition (see Fig. 1).

Further, our hypothesized distinction between stable and variable affordances anchored to the ventro-dorsal and dorso-dorsal sub-division may map onto the notion of dedicated circuits for reaching and grasping (see Borghi and Riggio, 2015; for a detailed discussion). Manual prehension involves a reach component, guiding the hand toward the object on the basis of its extrinsic features such as distance and direction, and a grasp component, shaping the fingers around the center of mass of the object on the basis of its intrinsic features such as size and shape of the object (Jeannerod, 1988). This functional distinction has been linked to a dorso-medial "reaching" circuit (Burnod et al., 1999) and a dorso-lateral "grasping" circuit (Jeannerod et al., 1995), connecting occipito-parietal cortex with the dorsal premotor cortex and anterior intraparietal cortex with the ventral premotor cortex, respectively (Galletti et al., 2003; Tanné-Gariépy et al., 2002). Transferred to our nomenclature, the "grasping" circuit corresponds preferably to the ventro-dorsal stream, which we dedicate to stable (including canonical) affordances, whereas the "reaching" circuit is related to the dorso-dorsal stream which underlies variable affordances and thus represents in particular the online control of object-related actions (see Fig. 1). This is in line with the proposal by Grol et al. (2007) that the two dorsal pathways might differ in the degree of online control required for a movement. A fundamental difference concerns the affordance concept in principle. Since affordances cannot be assimilated to object properties, intrinsic and extrinsic object properties cannot be one-to-one related to stable and variable affordances. Affordances rather indicate "action possibilities" as characterized by object properties the environment provides to the interacting organism. Hence, stable and variable affordances can emerge both during the reaching and the grasping action component. However, since most of the studies included in our meta-analysis did not contain a pure reaching component separated from a pure grasping component, our data does not enable us to answer this question on relationships between stable and variable affordances related to grasping and reaching components.

We have tried to spotlight the contribution of pure perceptual tasks and action-related tasks on the processing of different types of affordances. A large number of studies applied mere action observation tasks instructions, but we also included studies that required overt execution of object-directed actions or the active imagination of such actions. Since affordances denote the action possibilities afforded by an object and relate to both perception and action, i.e., refer to sensory-motor processes emerging from goal-directed object interaction, all of the included task instructions very likely reveal affordance processing. However, studies employing overt action may also reveal areas involved in rather pure action control (independent of more psychological processes, like affordances) or the degree of precision required by the movements (e.g., Grol et al., 2007). In the face of less and rather marginal statistical power (see Eickhoff et al., 2016), we found distinct activation patterns for stable versus variable affordances in visual perception tasks that were quite comparable to the main meta-analyses including all studies (see Appendix A inclusive of Fig. A1 and Table A1). Stable affordances revealed pronounced left-hemispheric activation clusters comprising inferior parietal cortex and frontal cortex, whereas variable affordances yielded rather dorsally located parieto-frontal activation clusters. In contrast, the activation patterns in visual action tasks differed to that in visual perception tasks, in particular for stable affordances. We found no activation in the posterior middle temporal gyrus and the ventral precentral gyrus for stable affordances in visual action tasks. Twenty-two out of the 44 studies classified as stable included action execution (some of the studies involved both a perception, i.e., observation condition and an action execution condition). Eleven of the studies including action observation involved reach-to-grasp movements of the arm. Only 4 of the other 11 studies employing tool-use pantomime, mime of gestures, or hand-object-interaction involved solely the hand. Since arm movements are predominantly loaded on the dorso-dorsal stream, this difference seems to be reasonable.

4.4. Implications for cognitive psychology

Our meta-analytic findings have at least two additional noteworthy theoretical implications: (1) they contribute to the long-lasting debate on the automaticity of affordance activation and (2) they lead to interesting hypotheses related to the time course of activation of different object characteristics. Previous evidence obtained by a number of behavioral studies manipulating the orientation of objects (for a seminal study, see Tucker and Ellis, 1998) and object parts (e.g., Phillips and Ward, 2002) suggests that affordances are activated independently of the task, yet are modulated by the task (Tipper et al., 2006; see also Pellicano et al., 2010). Our finding of two distinct anatomical-functional pathways, likely involved in parallel while responding to affordances and including potentially different activation time-courses, suggests that automaticity and timing of activation might differ depending on the kind of affordance. More specifically, in “offline” tasks, such as categorization in object recognition and language processing, stable affordances (as part of object representation) might be activated early on, while the activation timeline in online tasks, for instance during object-directed action, would be different: we namely predict that variable affordances are activated earlier than stable ones (see also Borghi, 2013; Myachykov et al., 2013, for work on language and affordances). In summation, the timing of affordance activation should be modulated by the task: in “offline” tasks we expect an early activation of stable affordances, in online tasks an early and automatic activation of variable ones (see Fig. 1). Thus, we do not think it is possible to speak of affordance automaticity overall, but to consider different kinds of affordances in relation to different kinds of tasks. Consider that some authors limit the use of the term affordance to the grasping circuit (e.g., Orban and Caruana, 2014), differentiating between grasping affordances and tool use. Even if we agree that the manipulation circuit and the use circuit are different, we extend the term affordance to cover both human object manipulation/grasping and human object use, because the distinction is not always clear. This allows us to speak of affordance activation during language processing in humans (for more extensive discussion of this issue, see Borghi and Riggio, 2015).

4.5. Affordances and the mirror neuron system

Affordances have further implications into the MNS. The MNS −comprising primarily the caudal part of inferior frontal gyrus (Area 44), ventral premotor cortex, and rostral part of inferior parietal lobule and known to be active during both action execution and observation– has been hypothesized to play various functional roles in, most prominently, action and intention understanding as well as imitation (e.g., Gallese et al., 2004; Rizzolatti and Craighero, 2004; Rizzolatti, 2005; but see also Hickok, 2013, 2009, for important caveats). Interestingly, meta-analytic findings by Caspers et al. (2010) revealed a bilateral network within frontal premotor, parietal, and temporo-occipital cortex involved in both action observation and imitation. The most consistently activated area was found in rostral inferior parietal cortex, corresponding to cytoarchitectonical area IPC (PFt), thus providing evidence for a possible homology of this region to area PF in non-human primates (see also Orban and Caruana, 2014; and recent data by Horoufchin et al., in preparation, showing differential activation for processing of new object concepts in anterior intraparietal sulcus and anterior supramarginal gyrus). Fogassi et al. (2005) have shown that mirror neurons in the convexity of inferior parietal lobe (PF/PFG complex) in monkeys appear to encode both specific motor components of an action (e.g., grasping) and the *overall* goal of the observed motor act (e.g., eating). Against this background, when an agent observes another interacting with an object, processing of the affordances involved in this object interaction is probable and may facilitate the understanding of the agents’ intention and thus the goal of the observed action. It follows that the mirror neuron and affordance systems are related. This is supported by the inclusion of some −albeit usually very abstracted[1]– affordance processing in most computational models of the MNS (e.g., Bonaiuto and Arbib, 2010; Bonaiuto et al., 2007; Oztop and Arbib, 2002; Thill et al., 2011). As suggested by Thill et al. (2013), this relationship consists of (1) the MNS guiding processes of learning suitable affordances with its representations of desired goals, and (2) the affordance system, in turn, being pivotal in the acquisition of suitable sensorimotor mappings to achieve these goals. This process may therefore involve distinct roles for functional and manipulative affordances, which are, as previously discussed, related to stable and variable affordances (Binkofski and Buxbaum, 2013). Our identification of their neural correlates can thus contribute to elucidating the precise relationship between mirror neuron and affordance systems, even if this remains a relatively unexplored area.

5. Conclusion

Our meta-analytic review provides evidence that the distinction between stable and variable affordances is well-grounded. We identified distinct neural pathways underlying stable and variable affordances and presented a first step towards a variety of research questions in cognitive neuroscience, for instance on the understanding of how stable and variable affordances are activated during “offline” and online tasks (e.g., during categorization in object recognition and language processing as well as during object-directed action respectively). Further research is needed to explore these fascinating topics and is certain to lead to new insights into the processing of affordances, which will in turn stimulate research in other areas.

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[1] It is, however, worth mentioning that neuroscientific data on distinct affordance processing pathways is nonetheless often taken into account for the implementation of these computational models in robots (see for example work on robot affordance processing, Koppula et al., 2013; see also Thill et al., 2013; for more thorough discussion of implications for robotics).

Appendix A. Effects for processing stable versus variable affordances in visual perception tasks

Effects for processing stable versus variable affordances in visual perception tasks

The meta-analysis for stable affordances in visual perception tasks was based on 71 experiments with 454 unique subjects (average of 16.2 subjects per experiment), and the meta-analysis for variable affordances in visual action tasks implied 50 experiments with 230 unique subjects (average of 12.3 subjects per experiment). This high degree of contribution related to the overall studies sample resulted in an activation pattern likewise already reported for processing stable versus variable affordances including all reported contrasts.

To sum up shortly, stable affordances in visual perception tasks yielded an activation pattern comprising parieto-frontal and temporo-occiptal clusters, which were more pronounced in the left hemisphere. Variable affordances in visual perception tasks revealed bilateral activations in superior parietal lobule (SPL (7A)), in addition to activation clusters in bilateral superior/middle frontal gyrus and right temporal gyrus. Conjunctive activations were found bilaterally in superior parietal lobule and superior/middle frontal gyrus, as well as in right temporal gyrus. The difference analysis STABLE > VARIABLE revealed pronounced left-hemispheric activation clusters comprising inferior parietal lobule and precentral gyrus, whereas the opposing direct contrast VARIABLE > STABLE showed dorsally located precentral and postcentral activation clusters.

Effects for processing stable versus variable affordances in visual action tasks

The meta-analyses including visual action tasks revealed a distinctive activation pattern for processing stable as compared to variable affordances. In detail, stable affordances revealed bilateral but stronger left-hemispheric activation in postcentral gyrus (Area 2) additionally to an activation in left middle frontal gyrus. We found no activation in the posterior middle temporal gyrus and the ventral precentral gyrus compared to the analysis for stable affordances in visual perception tasks. This difference seems to be reasonable, as most of the action execution studies involved reach-to-grasp arm movements that predominantly load on the dorso-dorsal stream (see also our discussion in the main text). In contrast, variable affordances yielded predominantly right-hemispheric activations, specifically, in right inferior parietal lobule (Area 2), in bilateral superior parietal lobule (SPL (7A)), in right supramarginal gyrus (IPC (PFcm)), and in right supplementary motor area (Area 6). Due to the lack of statistical power, no significant overlapping activations were revealed by a conjunction analysis STABLE ∩ VARIABLE. Note that the meta-analysis for stable affordances in visual action tasks included 17 experiments with 132 unique subjects (average of 15.1 subjects per experiment), whereas 9 experiments with 44 unique subjects (average of 10.2 subjects per experiment) were just entered in the meta-analysis for variable affordances in visual action tasks .

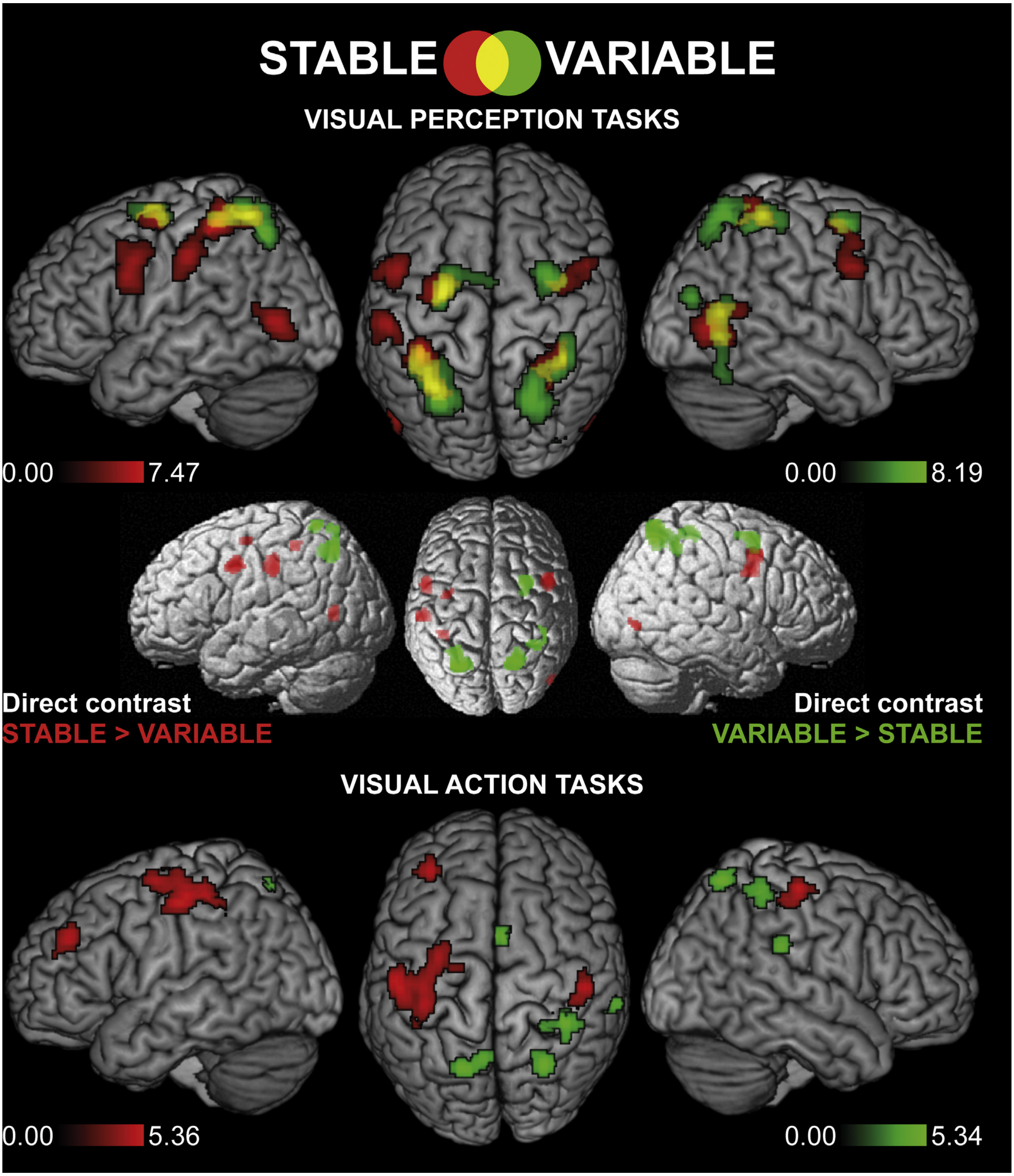

Fig. A1. Main effect of both stable affordances (red) and variable affordances (green) separately for visual perception tasks (top panel) and visual action tasks (bottom panel), as well as for visual perception tasks conjunctive activations (yellow) and differences as revealed by the direct contrasts stable affordances versus variable affordances. The statistical images were thresholded at $p < 0.05$, FWE corrected for the cluster level, superimposed on left, top, and right views of the volume rendered MNI template using the software MRIcron Version 06/2013 (http://www.nitrc.org/projects/mricron/). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table A1
Macroanatomical structure, cytoarchitectonic area ($\text{Area}_{\text{cyto}}$), percent overlap of cluster with cytoarchitectonic area, cluster size in voxel, MNI coordinates (x, y, z), and maximum T value (T_{max}) of the local maxima from both main effect of stable affordances and main effect of variable affordances separately for visual perception tasks and visual action tasks as well as the conjunction analysis, and the direct contrasts stable affordances versus variable affordances for visual perception tasks. The significance level was set to $p < 0.05$, FWE-corrected for the cluster level. Abbreviations: L. = left, R. = right.

Local maximum in macroanatomical structure	$\text{Area}_{\text{cyto}}$	Percent overlap of cluster with cytoarchitectonic area	Cluster size (voxel)	MNI coordinates			T_{max}
				x	y	z	
Main effect STABLE – Visual perception tasks							
L. Postcentral Gyrus	Area 2	37.5	1262	−38	−40	54	7.50
L. Inferior Parietal Lobule[a]	IPC (PFt)	16.4		−54	−24	38	6.16
L. Superior Parietal Lobule[a]	SPL (7A)	15.6		−30	−58	60	5.40
R. Middle Temporal Gyrus			586	48	−72	0	6.07
L. Inferior Frontal Gyrus (Pars opercularis)	Area 44	33.0	581	−48	8	28	5.79
L. Precentral Gyrus[a]				−50	4	36	5.75
R. Superior Parietal Lobule	Area 2	58.6	480	36	−44	60	5.35
R. Precentral Gyrus			460	46	4	32	5.87
L. Middle Occipital Gyrus	hOC5 (V5)	14.0	407	−46	−72	4	6.18
L. Precentral Gyrus			364	−28	−8	58	6.31
R. Fusiform Gyrus			120	40	−52	−20	4.39
Main effect VARIABLE – Visual perception tasks							
R. Superior Parietal Lobule	SPL (7A)	29.5	1252	20	−64	60	6.13
L. Superior Parietal Lobule			1057	−28	−64	48	8.22
L. Superior Parietal Lobule[a]	SPL (7A)	48.2		−32	−56	62	6.55
L. Superior Frontal Gyrus	Area 6	47.1	523	−26	−10	60	5.98
R. Middle Temporal Gyrus			469	48	−64	10	4.70
R. Inferior Temporal Gyrus[a]				46	−66	−6	4.55
R. Middle Frontal Gyrus			338	30	0	54	6.03
R. Middle Occipital Gyrus			119	32	−80	16	5.32
Conjunction STABLE ∩ VARIABLE – Visual perception tasks							
L. Superior Parietal Lobule	SPL (7A)	43.2	409	−30	−58	60	5.40
L. Superior Parietal Lobule[a]	SPL (7PC)	20.9		−34	−48	62	4.66
L. Superior Parietal Lobule[a]	Area 2	26.6		−40	−46	58	4.39
R. Middle Temporal Gyrus			225	48	−64	8	4.62
R. Inferior Temporal Gyrus[a]				46	−66	−4	4.48
L. Superior Frontal Gyrus			219	−26	−8	60	5.83
R. Postcentral Gyrus	Area 2	47.1	210	38	−42	60	4.83
R. Superior Parietal Lobule[a]	SPL (7PC)	18.7		26	−50	60	3.66
R. Middle Frontal Gyrus			60	36	−4	56	3.94
Direct contrast STABLE > VARIABLE – Visual perception tasks							
R. Precentral Gyrus			164[b]	46	0	38	3.09
L. Inferior Parietal Lobule	IPC (PFt)	67.1	98	−54	−26	36	2.77
L. Precentral Gyrus	Area 6	46.9	77	−54	2	40	3.02
L. Middle Temporal Gyrus			47	−44	−66	8	2.26
L. Inferior Parietal Lobule			27	−40	−40	52	1.93
L. Precentral Gyrus	Area 6	43.8	26	−38	−10	56	2.01
R. Inferior Occipital Gyrus			22	50	−78	−2	2.04
Direct contrast VARIABLE > STABLE – Visual perception tasks							
R. Precentral Gyrus	Area 6	3.4	164[b]	48	0	44	3.11
R. Postcentral Gyrus	Area 3b	17.3	13	30	−36	50	1.96
Main effect STABLE – Visual action tasks							
L. Postcentral Gyrus	Area 2	19.1	957	−52	−20	48	5.24
R. Postcentral Gyrus	Area 1	44.7	162	48	−24	56	5.14
L. Middle Frontal Gyrus			136	−34	38	30	4.78
R. Cerebellum	Lobule VI (Hem)	75.9	110	22	−50	−22	5.38
Main effect VARIABLE – Visual action tasks							
R. Inferior Parietal Lobule	Area 2	68.1	263	38	−42	52	5.00
L. Superior Parietal Lobule	SPL (7A)	90.6	172	−16	−66	56	4.92
R. SupraMarginal Gyrus	IPC (PFcm)	54.2	133	54	−34	26	4.51
R. Superior Parietal Lobule	SPL (7A)	88.7	124	26	−64	60	5.06
R. Supplementary Motor Area (SMA)	Area 6	94.7	102	6	4	54	5.36

[a] Note that for some activation clusters we report more than the first maxima. Sub-maxima are indicated by an asterisk.
[b] Indicates one cluster with two sub-maxima.

References

Ambron, E., Lingnau, A., Lunardelli, A., Pesavento, V., Rumiati, R.I., 2015. The effect of goals and vision on movements: a case study of optic ataxia and limb apraxia. Brain Cogn. 95, 77–89.

Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H.B., Zilles, K., 1999. Broca's region revisited: cytoarchitecture and intersubject variability. J. Comp. Neurol. 412 (2), 319–341.

Bálint, D., 1909. Seelenlähmung des Schauens, optische Ataxie, räumliche Störung der Aufmerksamkeit. Eur. Neurol. 25 (1), 51–81, German.

Begliomini, C., Wall, M.B., Smith, A.T., Castiello, U., 2007. Differential cortical activity for precision and whole-hand visually guided grasping in humans. Eur. J. Neurosci. 25 (4), 1245–1252.

Biagi, L., Cioni, G., Fogassi, L., Guzzetta, A., Tosetti, M., 2010. Anterior intraparietal cortex codes complexity of observed hand movements. Brain Res. Bull. 81 (4-5), 434–440.

Binkofski, F., Buxbaum, L.J., 2013. Two action systems in the human brain. Brain Lang. 127 (2), 222–229.

Binkofski, F., Fink, G., 2005. Apraxien [Apraxias]. Nervenarzt 76 (4), 493–509, quiz 510–511. German.

Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz, R.J., Freund, H.J., 1998. Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. Neurology 50 (5), 1253–1259.

Binkofski, F., Reetz, K., Blangero, A., 2007. Tactile agnosia and tactile apraxia: cross talk between the action and perception streams in the anterior intraparietal area. Behav. Brain Sci. 30, 201–202.

Bolognini, N., Convento, S., Banco, E., Mattioli, F., Tesio, L., Vallar, G., 2015. Improving ideomotor limb apraxia by electrical stimulation of the left posterior parietal cortex. Brain 138 (Pt 2), 428–439.

Bonaiuto, J., Arbib, M.A., 2010. Extending the mirror neuron system model, II: what did I just do? A new role for mirror neurons. Biol. Cybern. 102 (4), 341–359.

Bonaiuto, J., Rosta, E., Arbib, M., 2007. Extending the mirror neuron system model, I. Audible actions and invisible grasps. Biol. Cybern. 96 (1), 9–38.

Borchers, S., Müller, L., Synofzik, M., Himmelbach, M., 2013. Guidelines and quality measures for the diagnosis of optic ataxia. Front. Hum. Neurosci. 7, 324.

Borghi, A.M., Riggio, L., 2009. Sentence comprehension and simulation of object temporary, canonical and stable affordances. Brain Res. 1253, 117–128.

Borghi, A.M., Riggio, L., 2015. Stable and variable affordances are both automatic and flexible. Front. Hum. Neurosci. 9, 351.

Borghi, A.M., Binkofski, F., Buccino, G., Menz, M.M., Riggio, L., Sahin, E., Thill, S., Ziemke, T., 2010. Stable and variable affordances in the ROSSI project. In: Poster at the 4th International Conference on Cognitive Systems (CogSys 2010), January 27 and 28 2010 Zurich, Switzerland.

Borghi, A.M., Flumini, A., Natraj, N., Wheaton, L.A., 2012. One hand, two objects: emergence of affordance in contexts. Brain Cogn. 80 (1), 64–73.

Borghi, A.M., 2013. Action language comprehension, affordances and goals. In: Coello, Y., Bartolo, A. (Eds.), Language and Action in Cognitive Neuroscience: Contemporary Topics in Cognitive Neuroscience Series. Psychology Press, Hove (U.K.), pp. 125–143.

Boronat, C.B., Buxbaum, L.J., Coslett, H.B., Tang, K., Saffran, E.M., Kimberg, D.Y., Detre, J.A., 2005. Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. Brain Res. Cogn. Brain Res. 23 (2–3), 361–373.

Braadbaart, L., Williams, J.H., Waiter, G.D., 2013. Do mirror neuron areas mediate mu rhythm suppression during imitation and action observation? Int. J. Psychophysiol. 89 (1), 99–105.

Bub, D.N., Masson, M.E., Cree, G.S., 2008. Evocation of functional and volumetric gestural knowledge by objects and words. Cognition 106 (1), 27–58.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., Freund, H.J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur. J. Neurosci. 13 (2), 400–404.

Buccino, G., Binkofski, F., Riggio, L., 2004. The mirror neuron system and action recognition. Brain Lang. 89 (2), 370–376.

Burnod, Y., Baraduc, P., Battaglia-Mayer, A., Guigon, E., Koechlin, E., Ferraina, S., Lacquaniti, F., Caminiti, R., 1999. Parieto-frontal coding of reaching: an integrated framework. Exp. Brain Res. 129 (3), 325–346.

Buxbaum, L.J., Kalénine, S., 2010. Action knowledge, visuomotor activation, and embodiment in the two action systems. Ann. N. Y. Acad. Sci. 1191, 201–218.

Buxbaum, L.J., Johnson-Frey, S.H., Bartlett-Williams, M., 2005. Deficient internal models for planning hand-object interactions in apraxia. Neuropsychologia 43 (6), 917–929.

Buxbaum, L.J., Kyle, K.M., Tang, K., Detre, J.A., 2006. Neural substrates of knowledge of hand postures for object grasping and functional object use: evidence from fMRI. Brain Res. 1117 (1), 175–185.

Canessa, N., Borgo, F., Cappa, S.F., Perani, D., Falini, A., Buccino, G., Tettamanti, M., Shallice, T., 2008. The different neural correlates of action and functional knowledge in semantic memory: an FMRI study. Cereb. Cortex 18 (4), 740–751.

Cantagallo, A., Maini, M., Rumiati, R.I., 2012. The cognitive rehabilitation of limb apraxia in patients with stroke. Neuropsychol. Rehabil. 22 (3), 473–488.

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., Zilles, K., 2006. The human inferior parietal cortex: cytoarchitectonic parcellation and interindividual variability. Neuroimage 33 (2), 430–448.

Caspers, S., Eickhoff, S.B., Geyer, S., Scheperjans, F., Mohlberg, H., Zilles, K., Amunts, K., 2008. The human inferior parietal lobule in stereotaxic space. Brain Struct. Funct. 212 (6), 481–495.

Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action observation and imitation in the human brain. Neuroimage 50 (3), 1148–1167.

Cavina-Pratesi, C., Goodale, M.A., Culham, J.C., 2007. FMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. PLoS One 2 (5), e424.

Chapman, H., Gavrilescu, M., Wang, H., Kean, M., Egan, G., Castiello, U., 2002. Posterior parietal cortex control of reach-to-grasp movements in humans. Eur. J. Neurosci. 15 (12), 2037–2042.

Choi, S.H., Na, D.L., Kang, E., Lee, K.M., Lee, S.W., Na, D.G., 2001. Functional magnetic resonance imaging during pantomiming tool-use gestures. Exp. Brain Res. 139 (3), 311–317.

Chong, T.T., Williams, M.A., Cunnington, R., Mattingley, J.B., 2008. Selective attention modulates inferior frontal gyrus activity during action observation. Neuroimage 40 (1), 298–307.

Chouinard, P.A., Large, M.E., Chang, E.C., Goodale, M.A., 2009. Dissociable neural mechanisms for determining the perceived heaviness of objects and the predicted weight of objects during lifting: an fMRI investigation of the size-weight illusion. Neuroimage 44 (1), 200–212.

Costantini, M., Ambrosini, E., Scorolli, C., Borghi, A.M., 2011. When objects are close to me: affordances in the peripersonal space. Psychon. Bull. Rev. 18 (2), 302–308.

Creem-Regehr, S.H., Lee, J.N., 2005. Neural representations of graspable objects: are tools special? Brain Res. Cogn. Brain Res. 22 (3), 457–469.

Culham, J.C., Danckert, S.L., DeSouza, J.F., Gati, J.S., Menon, R.S., Goodale, M.A., 2003. Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. Exp. Brain Res. 153 (2), 180–189.

Daprati, E., Sirigu, A., 2006. How we interact with objects: learning from brain lesions. Trends Cogn. Sci. 10 (6), 265–270.

Derbyshire, N., Ellis, R., Tucker, M., 2006. The potentiation of two components of the reach-to-grasp action during object categorisation in visual memory. Acta Psychol. (Amst.) 122, 74–98.

Di Dio, C., Di Cesare, G., Higuchi, S., Roberts, N., Vogt, S., Rizzolatti, G., 2013. The neural correlates of velocity processing during the observation of a biological effector in the parietal and premotor cortex. Neuroimage 64, 425–436.

Diedrichsen, J., Balsters, J.H., Flavell, J., Cussans, E., Ramnani, N., 2009. A probabilistic MR atlas of the human cerebellum. Neuroimage 46 (1), 39–46.

Dovern, A., Fink, G.R., Weiss, P.H., 2012. Diagnosis and treatment of upper limb apraxia. J. Neurol. 259 (7), 1269–1283.

Ehrsson, H.H., Fagergren, A., Ehrsson, G.O., Forssberg, H., 2007. Holding an object: neural activity associated with fingertip force adjustments to external perturbations. J. Neurophysiol. 97 (2), 1342–1352.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25 (4), 1325–1335.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.H., Evans, A., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. Neuroimage 36 (3), 511–521.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum. Brain Mapp. 30 (9), 2907–2926.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Roski, C., Caspers, S., Zilles, K., Fox, P.T., 2011. Co-activation patterns distinguish cortical modules, their connectivity and functional differentiation. Neuroimage 57 (3), 938–949.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. Neuroimage 59 (3), 2349–2361.

Eickhoff, S.B., Nichols, T.E., Laird, A.R., Hoffstaedter, F., Amunts, K., Fox, P.T., Bzdok, D., Eickhoff, C.R., 2016. Behavior, Sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. Neuroimage (in press).

Ellis, R., Tucker, M., 2000. Micro-affordance: the potentiation of components of action by seen objects. Br. J. Psychol. 91 (Pt 4), 451–471.

Fabbri, S., Strnad, L., Caramazza, A., Lingnau, A., 2014. Overlapping representations for grip type and reach direction. Neuroimage 94, 138–146.

Faillenot, I., Sunaert, S., Van Hecke, P., Orban, G.A., 2001. Orientation discrimination of objects and gratings compared: an fMRI study. Eur. J. Neurosci. 13 (3), 585–596.

Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I., 2007. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. Neuroimage 37 (4), 1315–1328.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., Rizzolatti, G., 1996. Coding of peripersonal space in inferior premotor cortex (area F4). J. Neurophysiol. 76 (1), 141–157.

Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. Science 308 (5722), 662–667.

Frey, S.H., Vinton, D., Norlund, R., Grafton, S.T., 2005. Cortical topography of human anterior intraparietal cortex active during visually guided grasping. Brain Res. Cogn. Brain Res. 23 (2–3), 397–405.

Fridman, E.A., Immisch, I., Hanakawa, T., Bohlhalter, S., Waldvogel, D., Kansaku, K., Wheaton, L., Wu, T., Hallett, M., 2006. The role of the dorsal stream for gesture production. Neuroimage 29 (2), 417–428.

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain 119 (Pt 2), 593–609.

Gallese, V., Craighero, L., Fadiga, L., Fogassi, L., 1999. Perception through action. Psyche 5, 5–21.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8 (9), 396–403.

Galletti, C., Kutz, D.F., Gamberini, M., Breveglieri, R., Fattori, P., 2003. Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. Exp. Brain Res. 153 (2), 158–170.

Gallivan, J.P., McLean, D.A., Culham, J.C., 2011a. Neuroimaging reveals enhanced activation in a reach-selective brain area for objects located within participants' typical hand workspaces. Neuropsychologia 49 (13), 3710–3721.

Gallivan, J.P., McLean, D.A., Valyear, K.F., Pettypiece, C.E., Culham, J.C., 2011b. Decoding action intentions from preparatory brain activity in human parieto-frontal networks. J. Neurosci. 31 (26), 9599–9610.

Gallivan, J.P., McLean, D.A., Flanagan, J.R., Culham, J.C., 2013. Where one hand meets the other: limb-specific and action-dependent movement plans decoded from preparatory signals in single human frontoparietal brain areas. J. Neurosci. 33 (5), 1991–2008.

Garcin, R., Rondot, P., de Recondo, J., 1967. [Optic ataxia localized in 2 left homonymous visual hemifields (clinical study with film presentation)]. Rev. Neurol. (Paris) 116 (6), 707–714, French.

Geyer, S., Schleicher, A., Zilles, K., 1999. Areas 3a, 3b, and 1 of human primary somatosensory cortex. Neuroimage 10 (1), 63–83.

Geyer, S., Schormann, T., Mohlberg, H., Zilles, K., 2000. Areas 3a, 3b, and 1 of human primary somatosensory cortex: part 2. Spatial normalization to standard anatomical space. Neuroimage 11 (6 Pt 1), 684–696.

Geyer, S., 2004. The microstructural border between the motor and the cognitive domain in the human cerebral cortex. Adv. Anat. Embryol. Cell Biol. 174 (I-VIII), 1–89.

Gibson, J.J., 1979. The Ecological Approach to Visual Perception. Houghton Mifflin, Boston (MA).

Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. Trends Neurosci. 15 (1), 20–25.

Goodale, M.A., Meenan, J.P., Bülthoff, H.H., Nicolle, D.A., Murphy, K.J., Racicot, C.I., 1994. Separate neural pathways for the visual analysis of object shape in perception and prehension. Curr. Biol. 4 (7), 604–610.

Goodkind, M., Eickhoff, S.B., Oathes, D.J., Jiang, Y., Chang, A., Jones-Hagata, L.B., Ortega, B.N., Zaiko, Y.V., Roach, E.L., Korgaonkar, M.S., Grieve, S.M., Galatzer-Levy, I., Fox, P.T., Etkin, A., 2015. Identification of a common neurobiological substrate for mental illness. JAMA Psychiatry 72 (4), 305–315.

Grèzes, J., Armony, J.L., Rowe, J., Passingham, R.E., 2003a. Activations related to mirror and canonical neurones in the human brain: an fMRI study. Neuroimage 18 (4), 928–937.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., Passingham, R.E., 2003b. Objects automatically potentiate action: an fMRI study of implicit processing. Eur. J. Neurosci. 17 (12), 2735–2740.

Grefkes, C., Geyer, S., Schormann, T., Roland, P., Zilles, K., 2001. Human somatosensory area 2: observer-independent cytoarchitectonic mapping, interindividual variability, and population map. Neuroimage 14 (3), 617–631.

Grol, M.J., Majdandzić, J., Stephan, K.E., Verhagen, L., Dijkerman, H.C., Bekkering, H., Verstraten, F.A., Toni, I., 2007. Parieto-frontal connectivity during visually guided grasping. J. Neurosci. 27 (44), 11877–11887.

Haaland, K.Y., Porch, B.E., Delaney, H.D., 1980. Limb apraxia and motor performance. Brain Lang. 9 (2), 315–323.

Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., Büchel, C., 2003. The human action recognition system and its relationship to Broca's area: an fMRI study. Neuroimage 19 (3), 637–644.

Hamzei, F., Läppchen, C.H., Glauche, V., Mader, I., Rijntjes, M., Weiller, C., 2012. Functional plasticity induced by mirror training: the mirror as the element connecting both hands to one hemisphere. Neurorehabil. Neural Repair 26 (5), 484–496.

Hattori, N., Shibasaki, H., Wheaton, L., Wu, T., Matsuhashi, M., Hallett, M., 2009. Discrete parieto-frontal functional connectivity related to grasping. J. Neurophysiol. 101 (3), 1267–1282.

Hermsdörfer, J., Terlinden, G., Mühlau, M., Goldenberg, G., Wohlschläger, A.M., 2007. Neural representations of pantomimed and actual tool use: evidence from an event-related fMRI study. Neuroimage 36 (Suppl. 2), T109–118.

Hickok, G., 2009. Eight problems for the mirror neuron theory of action understanding in monkeys and humans. J. Cogn. Neurosci. 21 (7), 1229–1243.

Hickok, G., 2013. Do mirror neurons subserve action understanding? Neurosci. Lett. 540, 56–58.

Himmelbach, M., Karnath, H.O., 2005. Dorsal and ventral stream interaction: contributions from optic ataxia. J. Cogn. Neurosci. 17 (4), 632–640.

Hirose, S., Hagura, N., Matsumura, M., Naito, E., 2010. Human rostral dorsal premotor cortex mediates graspability judgment of external objects by evaluating hand motor capability. Brain Res. 1313, 134–142.

Hoeren, M., Kaller, C.P., Glauche, V., Vry, M.S., Rijntjes, M., Hamzei, F., Weiller, C., 2013. Action semantics and movement characteristics engage distinct processing streams during the observation of tool use. Exp. Brain Res. 229 (2), 243–260.

Hoeren, M., Kümmerer, D., Bormann, T., Beume, L., Ludwig, V.M., Vry, M.S., Mader, I., Rijntjes, M., Kaller, C.P., Weiller, C., 2014. Neural bases of imitation and pantomime in acute stroke patients: distinct streams for praxis. Brain 137 (Pt 10), 2796–2810.

James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., Goodale, M.A., 2002. Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. Neuron 35 (4), 793–801.

Jax, S.A., Buxbaum, L.J., 2010. Response interference between functional and structural actions linked to the same familiar object. Cognition 115 (2), 350–355.

Jeannerod, M., Jacob, P., 2005. Visual cognition: a new look at the two-visual systems model. Neuropsychologia 43 (2), 301–312.

Jeannerod, M., Arbib, M.A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci. 18 (7), 314–320.

Jeannerod, M., 1988. The Neural and Behavioural Organization of Goal-directed Movements. Clarendon Press/Oxford University Press, New York (NY).

Jenmalm, P., Schmitz, C., Forssberg, H., Ehrsson, H.H., 2006. Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. J. Neurosci. 26 (35), 9015–9021.

Johnson, S.H., Rotte, M., Grafton, S.T., Hinrichs, H., Gazzaniga, M.S., Heinze, H.J., 2002. Selective activation of a parietofrontal circuit during implicitly imagined prehension. Neuroimage 17 (4), 1693–1704.

Johnson-Frey, S.H., Maloof, F.R., Newman-Norlund, R., Farrer, C., Inati, S., Grafton, S.T., 2003. Actions or hand-object interactions? human inferior frontal cortex and action observation. Neuron 39 (6), 1053–1058.

Johnson-Frey, S.H., Newman-Norlund, R., Grafton, S.T., 2005. A distributed left hemisphere network active during planning of everyday tool use skills. Cereb. Cortex 15 (6), 681–695.

Jordan, K., Heinze, H.J., Lutz, K., Kanowski, M., Jäncke, L., 2001. Cortical activations during the mental rotation of different visual objects. Neuroimage 13 (1), 143–152.

Karnath, H.O., Perenin, M.T., 2005. Cortical control of visually guided reaching: evidence from patients with optic ataxia. Cereb. Cortex 15 (10), 1561–1569.

Keehner, M., Guerin, S.A., Miller, M.B., Turk, D.J., Hegarty, M., 2006. Modulation of neural activity by angle of rotation during imagined spatial transformations. Neuroimage 33 (1), 391–398.

Khan, A.Z., Pisella, L., Vighetto, A., Cotton, F., Luauté, J., Boisson, D., Salemme, R., Crawford, J.D., Rossetti, Y., 2005. Optic ataxia errors depend on remapped, not viewed, target location. Nat. Neurosci. 8 (4), 418–420.

Klinke, M.E., Jónsdóttir, H., 2014. Smoking addiction in chronic obstructive pulmonary disease: integrating neurobiology and phenomenology through a review of the literature. Chron. Respir. Dis. 11 (4), 229–236.

Koppula, H.S., Gupta, R., Saxena, A., 2013. Learning human activities and object affordances from RGB-D videos. Int. J. Rob. Res. 32 (8), 951–970.

Króliczak, G., Cavina-Pratesi, C., Goodman, D.A., Culham, J.C., 2007. What does the brain do when you fake it? An FMRI study of pantomimed and real grasping. J. Neurophysiol. 97 (3), 2410–2422.

Laird, A.R., Eickhoff, S.B., Kurth, F., Fox, P.M., Uecker, A.M., Turner, J.A., Robinson, J.L., Lancaster, J.L., Fox, P.T., 2009. ALE meta-analysis workflows via the Brainmap database: progress towards a probabilistic functional brain atlas. Front. Neuroinform. 3, 23.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. Biometrics 33 (1), 159–174.

Malfait, N., Valyear, K.F., Culham, J.C., Anton, J.L., Brown, L.E., Gribble, P.L., 2010. fMRI activation during observation of others' reach errors. J. Cogn. Neurosci. 22 (7), 1493–1503.

Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Eickhoff, S.B., Wilms, M., Palomero-Gallagher, N., Armstrong, E., Zilles, K., 2007. Cytoarchitectonic analysis of the human extrastriate cortex in the region of V5/MT+: a probabilistic, stereotaxic map of area hOc5. Cereb. Cortex 17 (3), 562–574.

Martin, M., Beume, L., Kümmerer, D., Schmidt, C.S., Bormann, T., Dressing, A., Ludwig, V.M., Umarova, R.M., Mader, I., Rijntjes, M., Kaller, C.P., Weiller, C., 2015. Differential roles of ventral and dorsal streams for conceptual and production-related components of tool use in acute stroke patients. Cereb. Cortex (in press).

Mecklinger, A., Gruenewald, C., Weiskopf, N., Doeller, C.F., 2004. Motor affordance and its role for visual working memory: evidence from fMRI studies. Exp. Psychol. 51 (4), 258–269.

Menz, M.M., McNamara, A., Klemen, J., Binkofski, F., 2009. Dissociating networks of imitation. Hum. Brain Mapp. 30 (10), 3339–3350.

Milner, A.D., Goodale, M.A., 1995. The Visual Brain in Action. Oxford University Press, Oxford, U.K.

Milner, A.D., Goodale, M.A., 2008. Two visual systems re-viewed. Neuropsychologia 46 (3), 774–785.

Milner, A.D., Dijkerman, H.C., Pisella, L., McIntosh, R.D., Tilikete, C., Vighetto, A., Rossetti, Y., 2001. Grasping the past: delay can improve visuomotor performance. Curr. Biol. 11 (23), 1896–1901.

Milner, T.E., Franklin, D.W., Imamizu, H., Kawato, M., 2006. Central representation of dynamics when manipulating handheld objects. J. Neurophysiol. 95 (2), 893–901.

Molenberghs, P., Brander, C., Mattingley, J.B., Cunnington, R., 2010. The role of the superior temporal sulcus and the mirror neuron system in imitation. Hum. Brain Mapp. 31 (9), 1316–1326.

Molinari, E., Baraldi, P., Campanella, M., Duzzi, D., Nocetti, L., Pagnoni, G., Porro, C.A., 2013. Human parietofrontal networks related to action observation detected at rest. Cereb. Cortex 23 (1), 178–186.

Morrison, I., Tipper, S.P., Fenton-Adams, W.L., Bach, P., 2013. Feeling others' painful actions: the sensorimotor integration of pain and action information. Hum. Brain Mapp. 34 (8), 1982–1998.

Mosier, K., Lau, C., Wang, Y., Venkadesan, M., Valero-Cuevas, F.J., 2011. Controlling instabilities in manipulation requires specific cortical-striatal-cerebellar networks. J. Neurophysiol. 105 (3), 1295–1305.

Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., Rizzolatti, G., 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. J. Neurophysiol. 78, 2226–2230.

Myachykov, A., Ellis, R., Cangelosi, A., Fischer, M.H., 2013. Visual and linguistic cues to graspable objects. Exp. Brain Res. 229 (4), 545–559.

Natraj, N., Poole, V., Mizelle, J.C., Flumini, A., Borghi, A.M., Wheaton, L.A., 2013. Context and hand posture modulate the neural dynamics of tool-object perception. Neuropsychologia 51 (3), 506–519.

Nocchi, F., Gazzellini, S., Grisolia, C., Petrarca, M., Cannatà, V., Cappa, P., D'Alessio, T., Castelli, E., 2012. Brain network involved in visual processing of movement stimuli used in upper limb robotic training: an fMRI study. J. Neuroeng. Rehabil. 9, 49.

Ocampo, B., Kritikos, A., Cunnington, R., 2011. How frontoparietal brain regions mediate imitative and complementary actions: an FMRI study. PLoS One 6 (10), e26945.

Ogawa, K., Inui, T., 2012. Multiple neural representations of object-directed action in an imitative context. Exp. Brain Res. 216 (1), 61–69.

Oliver, R.T., Thompson-Schill, S.L., 2003. Dorsal stream activation during retrieval of object size and shape. Cogn. Affect. Behav. Neurosci. 3 (4), 309–322.

Oosterhof, N.N., Tipper, S.P., Downing, P.E., 2012. Visuo-motor imagery of specific manual actions: a multi-variate pattern analysis fMRI study. Neuroimage 63 (1), 262–271.

Orban, G.A., Caruana, F., 2014. The neural basis of human tool use. Front. Psychol. 5, 310.

Oztop, E., Arbib, M.A., 2002. Schema design and implementation of the grasp-related mirror neuron system. Biol. Cybern. 87 (2), 116–140.

Péran, P., Démonet, J.F., Cherubini, A., Carbebat, D., Caltagirone, C., Sabatini, U., 2010. Mental representations of action: the neural correlates of the verbal and motor components. Brain Res. 1328, 89–103.

Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2009. The representation of tool use in humans and monkeys: common and uniquely human features. J. Neurosci. 29 (37), 11523–11539.

Pellicano, A., Iani, C., Borghi, A.M., Rubichi, S., Nicoletti, R., 2010. Simon-like and functional affordance effects with tools: the effects of object perceptual discrimination and object action state. Q. J. Exp. Psychol. (Hove) 63 (11), 2190–2201.

Pellicano, A., Thill, S., Ziemke, T., Binkofski, F., 2011. Affordances, adaptive tool use and grounded cognition. Front. Psychol. 2, 53.

Perenin, M.T., Vighetto, A., 1988. Optic ataxia: a specific disruption in visuomotor mechanisms: I. Different aspects of the deficit in reaching for objects. Brain 111 (Pt 3), 643–674.

Phillips, J.C., Ward, R., 2002. S-R correspondence effects of irrelevant visual affordance: time course and specificity of response activation. Vis. Cogn. 9 (4–5), 540–558.

Pierno, A.C., Becchio, C., Wall, M.B., Smith, A.T., Castiello, U., 2006. Transfer of interfered motor patterns to self from others. Eur. J. Neurosci. 23 (7), 1949–1955.

Pierno, A.C., Tubaldi, F., Turella, L., Grossi, P., Barachino, L., Gallo, P., Castiello, U., 2009. Neurofunctional modulation of brain regions by the observation of pointing and grasping actions. Cereb. Cortex 19 (2), 367–374.

Pisella, L., Gréa, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., Rossetti, Y., 2000. An ‘automatic pilot’ for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. Nat. Neurosci. 3 (7), 729–736.

Pisella, L., Binkofski, F., Lasek, K., Toni, I., Rossetti, Y., 2006. No double-dissociation between optic ataxia and visual agnosia: multiple sub-streams for multiple visuo-manual integrations. Neuropsychologia 44 (13), 2734–2748.

Prablanc, C., Desmurget, M., Gréa, H., 2003. Neural control of on-line guidance of hand reaching movements. Prog. Brain Res. 142, 155–170.

Randolph, J.J., 2005. Free-marginal multirater kappa: an alternative to Fleiss' fixed-marginal multirater kappa. In: Paper Presented at the Joensuu University Learning and Instruction Symposium 2005, Joensuu, Finland, October 14–15th (ERIC Document Reproduction Service No. ED490661).

Renzi, C., Ricciardi, E., Bonino, D., Handjaras, G., Vecchi, T., Pietrini, P., 2013. The effects of visual control and distance in modulating peripersonal spatial representation. PLoS One. 8 (3), e59460.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Rizzolatti, G., Fadiga, L., 1998. Grasping objects and grasping action meanings: the dual role of monkey rostroventral premotor cortex (area F5). Novartis Found Symp. 218, 81–95.

Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and functions. Exp. Brain Res. 153 (2), 146–157.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. Brain Res. Cogn. Brain Res. 3 (2), 131–141.

Rizzolatti, G., Luppino, G., Matelli, M., 1998. The organization of the cortical motor system: new concepts. Electroencephalogr. Clin. Neurophysiol. 106 (4), 283–296.

Rizzolatti, G., 2005. The mirror neuron system and its function in humans. Anat. Embryol. (Berl.) 210 (5–6), 419–421.

Rossetti, Y., Revol, P., McIntosh, R., Pisella, L., Rode, G., Danckert, J., Tilikete, C., Dijkerman, H.C., Boisson, D., Vighetto, A., Michel, F., Milner, A.D., 2005. Visually guided reaching: bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. Neuropsychologia 43 (2), 162–177.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A.R., Schulz, J.B., Fox, P.T., Eickhoff, S.B., 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. Neuroimage 60 (1), 830–846.

Rottschy, C., Caspers, S., Roski, C., Reetz, K., Dogan, I., Schulz, J.B., Zilles, K., Laird, A.R., Fox, P.T., Eickhoff, S.B., 2013. Differentiated parietal connectivity of frontal regions for what and where memory. Brain Struct. Funct. 218 (6), 1551–1567.

Sakaguchi, Y., Ishida, F., Shimizu, T., Murata, A., 2010. Time course of information representation of macaque AIP neurons in hand manipulation task revealed by information analysis. J. Neurophysiol. 104 (6), 3625–3643.

Scheperjans, F., Eickhoff, S.B., Hömke, L., Mohlberg, H., Hermann, K., Amunts, K., Zilles, K., 2008a. Probabilistic maps, morphometry, and variability of cytoarchitectonic areas in the human superior parietal cortex. Cereb. Cortex 18 (9), 2141–2157.

Scheperjans, F., Hermann, K., Eickhoff, S.B., Amunts, K., Schleicher, A., Zilles, K., 2008b. Observer-independent cytoarchitectonic mapping of the human superior parietal cortex. Cereb. Cortex 18 (4), 846–867.

Schubotz, R.I., Korb, F.M., Schiffer, A.M., Stadler, W., von Cramon, D.Y., 2012. The fraction of an action is more than a movement: neural signatures of event segmentation in fMRI. Neuroimage 61 (4), 1195–1205.

Shmuelof, L., Zohary, E., 2005. Dissociation between ventral and dorsal fMRI activation during object and action recognition. Neuron 47 (3), 457–470.

Shmuelof, L., Zohary, E., 2006. A mirror representation of others' actions in the human anterior parietal cortex. J. Neurosci. 26 (38), 9736–9742.

Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. Neuron 33 (3), 475–487.

Smania, N., Aglioti, S.M., Girardi, F., Tinazzi, M., Fiaschi, A., Cosentino, A., Corato, E., 2006. Rehabilitation of limb apraxia improves daily life activities in patients with stroke. Neurology 67 (11), 2050–2052.

Sugio, T., Inui, T., Matsuo, K., Matsuzawa, M., Glover, G.H., Nakai, T., 1999. The role of the posterior parietal cortex in human object recognition: a functional magnetic resonance imaging study. Neurosci. Lett. 276 (1), 45–48.

Tanné-Gariépy, J., Rouiller, E.M., Boussaoud, D., 2002. Parietal inputs to dorsal versus ventral premotor areas in the macaque monkey: evidence for largely segregated visuomotor pathways. Exp. Brain Res. 145 (1), 91–103.

Terhune, K.P., Liu, G.T., Modestino, E.J., Miki, A., Sheth, K.N., Liu, C.S., Bonhomme, G.R., Haselgrove, J.C., 2005. Recognition of objects in non-canonical views: a functional MRI study. J. Neuroophthalmol. 25 (4), 273–279.

Thill, S., Svensson, H., Ziemke, T., 2011. Modeling the development of goal-specificity in mirror neurons. Cognit. Comput. 3 (4), 525–538.

Thill, S., Caligiore, D., Borghi, A.M., Ziemke, T., Baldassarre, G., 2013. Theories and computational models of affordance and mirror systems: an integrative review. Neurosci. Biobehav. Rev. 37 (3), 491–521.

Tipper, S.P., Paul, M.A., Hayes, A.E., 2006. Vision-for-action: the effects of object property discrimination and action state on affordance compatibility effects. Psychon. Bull. Rev. 13 (3), 493–498.

Toyokura, M., Koike, T., 2006. Rehabilitative intervention and social participation of a case with Balint's syndrome and aphasia. Tokai J. Exp. Clin. Med. 31 (2), 78–82.

Tucker, M., Ellis, R., 1998. On the relations between seen objects and components of potential actions. J. Exp. Psychol. Hum. Percept. Perform. 24 (3), 830–846.

Tucker, M., Ellis, R., 2004. Action priming by briefly presented objects. Acta Psychol. (Amst.) 116 (2), 185–203.

Tunik, E., Frey, S.H., Grafton, S.T., 2005. Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. Nat. Neurosci. 8 (4), 505–511.

Turella, L., Erb, M., Grodd, W., Castiello, U., 2009. Visual features of an observed agent do not modulate human brain activity during action observation. Neuroimage 46 (3), 844–853.

Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in Activation Likelihood Estimation meta-analyses. Hum. Brain Mapp. 33 (1), 1–13.

Ungerleider, L.G., Haxby, J.V., 1994. 'What' and 'where' in the human brain. Curr. Opin. Neurobiol. 4 (2), 157–165.

Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of Visual Behavior. MIT Press, Cambridge (MA), pp. 549–586.

Valyear, K.F., Gallivan, J.P., McLean, D.A., Culham, J.C., 2012. fMRI repetition suppression for familiar but not arbitrary actions with tools. J. Neurosci. 32 (12), 4247–4259.

Vanrie, J., Béatse, E., Wagemans, J., Sunaert, S., Van Hecke, P., 2002. Mental rotation versus invariant features in object perception from different viewpoints: an fMRI study. Neuropsychologia 40 (7), 917–930.

Verhagen, L., Dijkerman, H.C., Medendorp, W.P., Toni, I., 2012. Cortical dynamics of sensorimotor integration during grasp planning. J. Neurosci. 32 (13), 4508–4519.

Vingerhoets, G., de Lange, F.P., Vandemaele, P., Deblaere, K., Achten, E., 2002. Motor imagery in mental rotation: an fMRI study. Neuroimage 17 (3), 1623–1633.

Vingerhoets, G., Vandekerckhove, E., Honoré, P., Vandemaele, P., Achten, E., 2011. Neural correlates of pantomiming familiar and unfamiliar tools: action semantics versus mechanical problem solving? Hum. Brain Mapp. 32 (6), 905–918.

Vingerhoets, G., Stevens, L., Meesdom, M., Honoré, P., Vandemaele, P., Achten, E., 2012. Influence of perspective on the neural correlates of motor resonance during natural action observation. Neuropsychol. Rehabil. 22 (5), 752–767.

Vingerhoets, G., Nys, J., Honoré, P., Vandekerckhove, E., Vandemaele, P., 2013. Human left ventral premotor cortex mediates matching of hand posture to object use. PLoS One 8 (7), e70480.

Wadsworth, H.M., Kana, R.K., 2011. Brain mechanisms of perceiving tools and imagining tool use acts: a functional MRI study. Neuropsychologia 49 (7), 1863–1869.

Warrens, M.J., 2010. Inequalities between multi-rater kappas. Adv. Data Anal. Classif. 4 (4), 271–286.

Watson, C.E., Buxbaum, L.J., 2015. A distributed network critical for selecting among tool-directed actions. Cortex 65, 65–82.

Yoon, E.Y., Humphreys, G.W., Kumar, S., Rotshtein, P., 2012. The neural selection and integration of actions and objects: an fMRI study. J. Cogn. Neurosci. 24 (11), 2268–2279.

Young, G., 2006. Are different affordances subserved by different neural pathways? Brain Cogn. 62 (2), 134–142.

Zacks, J.M., Vettel, J.M., Michelon, P., 2003. Imagined viewer and object rotations dissociated with event-related FMRI. J. Cogn. Neurosci. 15 (7), 1002–1018.