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Review

From Observed Action Identity to Social Affordances

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Others' observed actions cause continuously changing retinal images, making it challenging to build neural representations of action identity. The monkey anterior intraparietal area (AIP) and its putative human homologue (phAIP) host neurons selective for observed manipulative actions (OMAs). The neuronal activity of both AIP and phAIP allows a stable readout of OMA identity across visual formats, but human neurons exhibit greater invariance and generalize from observed actions to action verbs. These properties stem from the convergence in AIP of superior temporal signals concerning: (i) observed body movements; and (ii) the changes in the body–object relationship. We propose that evolutionarily preserved mechanisms underlie the specification of observed-actions identity and the selection of motor responses afforded by them, thereby promoting social behavior.

Combining Observed Body Movements and Objects Changes: The Action's Identity

Manual skills are a hallmark of primates, particularly humans. They have made possible most of our transformational impact on the world, which was driven by an evolutionarily preserved but expanding network of cortical areas in the primate lineage that subserves the neural control of manipulative actions [1–4]. Interestingly, an equally well-articulated neural machinery is required to resolve the visual complexity of **observed manipulative actions (OMAs)** (see Glossary) performed by other individuals, because this ability is of critical importance for action planning during social interaction and interindividual coordination [5–7]. Indeed, as compared with other complex static visual stimuli, such as objects [8], faces [9,10], others' gaze direction [11], and body posture [12], observed actions of others are inherently dynamic stimuli, and their dynamics are essential for an observer's brain to compute their identity, despite the rapid changes in their retinal image. This is probably the reason why James Gibson claimed that 'animals are by far the most complex objects of perception that the environment presents to an observer' [13].

Body movements are a fundamental component of an 'action'; nonetheless, they represent only one such component. In fact, an action is much more than a set of coordinated body movements, since it aims to produce a change in the environment in which the subject is immersed [14]. Thus, the changes an agent's action causes in the target object constitute an element that is almost as important as the body movement itself, because its dynamics make the OMA predictable in terms of its **motor goal** [15–17]. These two types of signal, specifying: (i) how the dynamics of body movement unfold; and (ii) how it will change the position or shape of an object, naturally coexist in everyday manipulative actions, and characterize the **action identity**. Both elements are crucial. For example, the same grasping act performed on a branch may serve to secure the body while climbing, to manipulate it for grabbing fruits, or to use it to hit something or someone else: in spite of the body-movement similarity, these clearly constitute different actions with different consequences. Similarly, the same effect of moving an object away from the body can be achieved by pushing it, throwing it, or kicking it, which clearly constitute different actions despite the similar consequence they produce in the outside world.

Highlights

A substantial fraction of neurons in the monkey anterior intraparietal area (AIP) and its human homologue phAIP are selective for observed manipulative actions (OMAs).

OMA selective neurons encode the identity of the observed actions, up to the level of semantic representation in phAIP.

OMA identity may result from the combination of two visual signals originating in the superior temporal sulcus (STS) and concerning: (i) observed body movements: and (ii) the changes in the hand/object relationship (action effects).

Others' observed actions, beyond grasping, may be specified in parietal territories, underpinning 'social affordance' processing and the selection of potential behavioral responses in parieto-premotor circuits.

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Here, we first review evidence of neuronal signatures of OMA-identity coding in the primate brain, which point to area AIP as a critical node for this function. We then elucidate the connectional architecture that enables the convergence and integration in AIP of the two main sources of information needed to encode OMA identity: body movements and hand–object-interaction signals (i.e., attainment of the motor goal). Finally, we propose an extension of this model to a larger variety of **action classes** beyond the manipulative ones and of parietal areas in addition to AIP, which should drive future studies on the neural mechanisms underlying the computation of action identity in the non-human and human primate brain.

OMA Identity in the Monkey and Human AIP

Area AIP has long been considered a crucial node of the cortical motor system because of its role in routing visual information regarding 3D objects [18–20] and observed actions [21,22] from temporal [23,24] and other parietal [25,26] regions to the premotor cortex [27], whereas neighboring inferior parietal convexity areas were deemed to play a more important role in the processing of other's observed actions [28,29]. Extant studies have focused almost exclusively on the neural coding of graspable objects and grasping actions, with the exception of recent investigations that have recorded AIP neuronal activity while monkeys observed a larger set of OMA exemplars [30,31]. The findings of these latter studies demonstrate a crucial role of area AIP in routing visual information about OMAs to the other nodes of the cortical action observation network.

What are the mechanisms through which the brain can achieve a stable readout of the identity of others' manipulative actions? In a recent study [31], AIP neurons displayed a marked selectivity for OMAs performed by another monkey (i.e., grasping and grooming) among a variety of stimuli, including emotional facial gestures (i.e., lip smacking and screaming), neutral facial gestures (i.e., yawning and chewing), and other dynamic stimuli (i.e., still monkey, a moving animal, and a landscape) presented on a screen. In that study, AIP neurons were also tested with a large set of OMA exemplars (i.e., dragging, dropping, grasping, pulling, pushing, rotating, and squeezing) previously used to reveal action-identity coding in monkey AIP [30]. In addition, OMA exemplars were presented in four visual formats, resulting from the combination of two body postures of an actor (standing and sitting) and two viewpoints (lateral and frontal) (Figure 1A). The results showed that 38% of AIP neurons showed selectivity for OMAs in at least one format, with distinct sets of neurons exhibiting a preference for a specific exemplar (or set of exemplars), in addition to tuning for the visual presentation format (see example neuron in Figure 1A). However, no neuron exhibiting fully visual-invariant OMA selectivity was found. In fact, information about visual format and action identity was dynamically integrated according to a **multiplicative mixing** model [31], as previously described for static images in the inferior temporal cortex [32]. Such a multiplicative mixing of visual information enables the decoding of an early signal about the viewpoint (50 ms after stimulus onset) and the actor's body posture (at 100 ms) and, slightly later (150 ms), even the decoding of OMA identity in a format-independent manner. Crucially, the accuracy with which OMA identity is decoded depends upon the presence of a subset of units that maintain a relatively stable OMA selectivity across formats despite considerable rescaling of their firing rate according to the visual specificities of each format (as in the example neuron of Figure 1A).

What is the relationship, if one exists, between neuronal representations of individual OMA exemplars in AIP? The clustering of individual exemplars in the neural space [31] indicated that actions characterized by the movement of the hand toward a target lying on a table (e.g., grasping or dragging) were more closely linked and, consequently, segregated from those in which the hand was already in contact with the manipulated object (e.g., rolling or squeezing, Figure 1B). This clustering of action exemplars was largely independent of the variety of combinations of viewpoints and body postures (Figure 1C), suggesting that the dynamic relationships between

(See figure legend at the bottom of the next page.)

the actor's hand and the target object, which are relatively stable across formats, make a fundamental contribution to the neural representation of OMA identity.

Interestingly, the same stimuli used to study monkey AIP neurons (Figure 1A) were recently presented to two human patients participating in a brain–machine interface clinical trial, allowing the researchers to record single-neuron activity from the rostral intraparietal sulcus [33], a region deemed to include the phAIP [34]. The findings revealed impressive similarities with those reported in monkeys. First, in each viewpoint, approximately 20% of phAIP neurons were OMA selective, as in the monkey: the majority of them showed facilitated response to OMAs (Figure 1D), whereas a smaller set (about 15%) were suppressed in both humans and monkeys. Second, phAIP neurons could be tuned to any of the exemplars tested, but coverage of OMA exemplars was more uniform in humans than in the monkeys. Third, OMA exemplars could be decoded from the phAIP population activity recorded in each of the two tested patients, providing significant information about the observed exemplar with the same latency reported in the monkey (150 ms from video onset). Finally, format-dependent coding was evident also among human neurons, and although it is difficult to reach a firm conclusion based on the available evidence, it is plausible that a multiplicative mixing of visual format and OMA-identity information has been preserved from the common ancestor of humans and monkeys. However, differently from the monkey AIP, a sizable fraction of human phAIP OMA-selective neurons exhibited format-invariant tuning (80% were posture invariant and 55% viewpoint invariant), which is consistent with the evidence of generalization across viewpoints during OMA-discrimination tasks in humans [35]. The greater invariance of human OMA-selective neurons may thus facilitate the recruitment of neural representations of observed actions, even by reading action verbs [33], a uniquely human capacity.

To summarize, human and non-human primates (i.e., macaques) have a remarkably similar neuronal machinery in homologue regions of the rostral intraparietal sulcus, which encode OMA identity at a variable degree of visual invariance and abstraction in order to access it, for example, via the human reading of written words [33]. The functional similarities between basic properties of monkey and human OMA-selective neurons raise the fundamental question of what the underlying anatomical architecture might be.

The Connectional Architecture Underlying OMA identity

The tuning for OMAs is prevalent in the caudal portion of AIP, a region where the influence of own-hand visual feedback and overall visual responsiveness was found to be stronger than in the rostral sector [30]. In that study, neural tracers were injected at three distinct positions along the rostro-caudal extent of the physiologically investigated region. The results confirmed previous anatomical findings [36] (Figure 2A) and revealed quantitative differences in the connectivity patterns between the caudal and rostral AIP (Figure 2B). In particular, the caudal part of AIP with stronger OMA

Figure 1. Examples of Monkey and Human Single Neurons. (A) Example stimuli of one of the seven OMAs (grasping) in each of the four visual formats tested in the monkey experiments; the rasters and histograms under each stimulus illustrate the response of a single-neuron example (with a preference for dropping, rolling, and squeezing, especially in the stand frontal viewpoint) recorded from the monkey AIP during the observation of each of the seven OMAs (color code) in each format. Histograms in the inset show the response (mean spk/s ± standard error) of the neuron to the seven OMAs in each format. (B) Clustering of OMA exemplars irrespective of the visual presentation format (n = 257 units). (C) Clustering of OMA exemplars within the same set of units but considering the different visual formats. (D) Example stimuli of one of the five OMAs (not the one preferred by the example neuron later) tested in human patients (the same as in the monkey) in three formats (tested in the monkey as well), in addition to the text format (last column); the panels under each stimulus show the time course of the firing rate (mean ± standard error) of a single neuron (with a preference for dragging in the two lateral viewpoints and text formats) recorded in phAIP for each tested OMA (color code) in each format. Reproduced with permission from [33]. Abbreviations: AIP, anterior intraparietal area; OMA, observed manipulative actions; phAIP, putative human homologue.
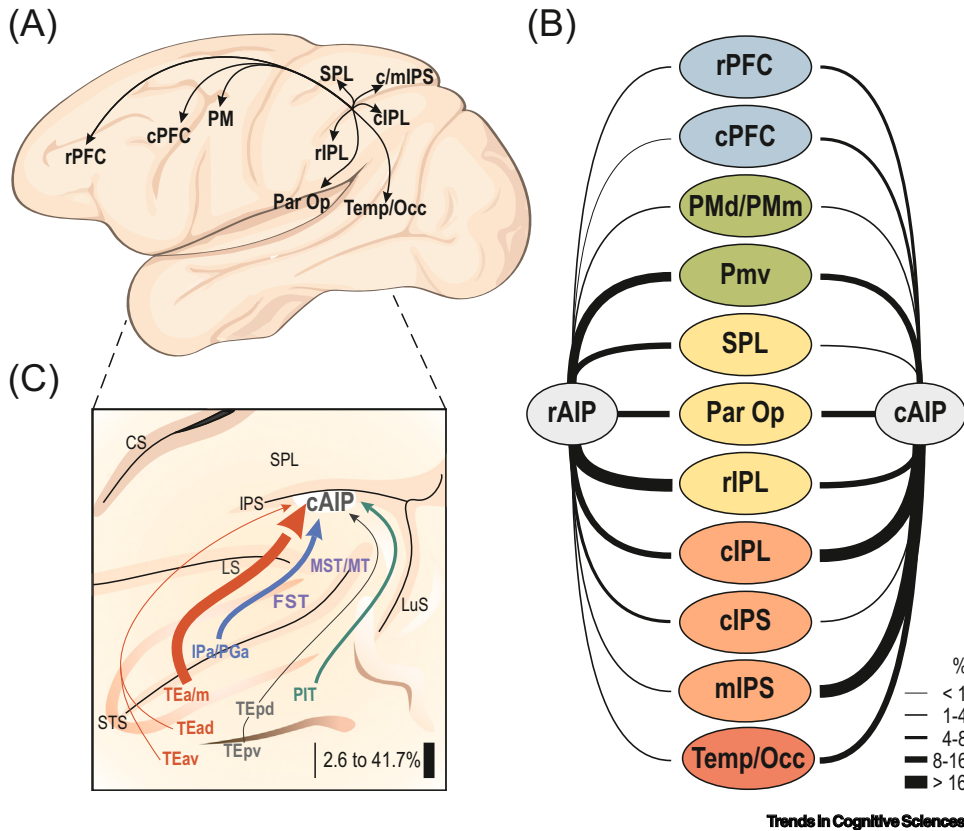
Figure 2. Connectional Architecture of the Monkey AIP. (A) Schematic representation of the main connectional pathways of area AIP (all cortico–cortical connections have to be considered as reciprocal). (B) Comparative strength of the connections of the rostral (rAIP) and caudal (cAIP) portion of AIP (percentage calculated over the total connections of the area). (C) Schematic representation of an unfolding of the temporal cortex showing the relative strength of projections to AIP among areas of the inferotemporal cortex (percentage calculated over the total connections with the temporal lobe). Abbreviations: AIP, anterior intraparietal area; CS, central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; LuS, lunate sulcus; SPL, superior parietal lobule.

selectivity, exhibited stronger connections with rostral and caudal prefrontal regions, caudal parietal convexity and lateral intraparietal area, and a variety of occipito-temporal regions (Figure 2C).

Although OMA-identity coding has yet to be investigated in brain regions other than AIP, previous neurophysiological studies [23] reported that neurons in the lower bank of the rostral superior temporal sulcus (STS), known as hand–object-interaction neurons, signal the relationship between a moving hand and its target. Indeed, the discharge of such neurons was lower when the hand or the target was presented in isolation or at some distance one from each other. Furthermore, some STS neurons responded when the observed hand was that of the recorded monkey, similarly to many AIP neurons [22,30]; such responses might enable monkeys to assess the consequences of their own hand–object interactions. Importantly, these responses were relatively unaffected by most properties of the object except its rigidity or food quality. Finally, these neurons responded also when tested with different body movements that resulted in similar effects on the object, suggesting that they essentially code the hand–object interaction rather than the observed action itself. The anatomical location of these STS neurons corresponds to area TEa [37], one of the most prominent sources of temporal projection to AIP, targeting mainly its caudal part, where OMA-selective neurons prevail [30]. Thus, the TEa–AIP pathway (red arrow

in Figure 2C) likely represents the source to AIP of visual information about the dynamics of hand–object interaction resulting from the observed manipulations.

Areas IPa/PGa (Figure 2C) represent another potentially relevant source of visual information about OMA identity. A study that approximately targeted this middle-STS region [38], reported neuronal selectivity for two features of observed forelimb actions, portrayed by stick figures: static posture and body-part deformation, encoded by 'snapshot' neurons and kinematic features, encoded by 'motion' neurons. These cells could provide a rich set of information about others' body-part movements, which are critical for extracting OMA identity. Importantly, another study recently showed that the middle-STS region is involved in the visual processing of social interactions [39,40], constituting a key node of the recently proposed 'third visual pathway' [41]. Thus far, there is little evidence for the view independence of middle-STS neurons. Indeed, middle-STS body-patch neurons display mostly view-dependent coding of body posture and identity [12], which is in line with previously reported properties of STS neurons encoding body movements (such as walking and bending the knee) [42]. Thus, IPa/PGa may provide view-dependent information regarding body movements to AIP (blue arrow in Figure 2C), coherently with the strong tuning for visual formats reported in monkey's AIP [31].

The anatomo-functional evidence reviewed in the preceding text suggests that the monkey's caudal area AIP receives from the STS two convergent sources of visual information relevant to OMA-identity processing (Figure 3, Key Figure): body-movement signals from IPa/PGa and hand–object-interaction signals from TEa. Considering the homology of STS regions [43], this scheme can be extended to humans. Indeed, the phAIP of the monkey TEa is located in the posterior occipitotemporal sulcus and extends into the fusiform gyrus [43]: this region may contribute to processing object changes caused by others' actions [44]. By contrast, the human homologue of the monkey IPa/PGa regions may be split between the posterior occipitotemporal sulcus and the posterior middle temporal gyrus, and extend into the posterior STS [43]; these regions correspond to the activations in the lateral and ventral temporal cortex during observation of body movements [45,46].

The Behavioral Role of OMA-Identity Coding

Why is OMA identity represented in primates' intraparietal cortex? As mentioned previously, in both humans and monkeys, OMA-selective neurons can show either facilitated or suppressed visual responses; however, when monkeys are tested during active execution of reaching–grasping actions in the dark, only facilitated neurons (not suppressed ones) also show a genuine motor response. On this basis, we proposed [30] that OMA-selective AIP visuomotor neurons provide signals for action planning based on the monkey's processing of what another is doing. This mechanism would work alongside the one previously described for object **affordances**. Indeed, the physical features of observed objects are represented in both parietal [18,21] and premotor [20,47,48] neurons, forming a parieto-frontal circuit with an experimentally established causal role in visually guided reaching–grasping actions [49,50]. According to our hypothesis, just as observed objects afford specific manual actions in the parieto-frontal system depending on their physical features and the environmental context [51], the observation of others' actions induces the observer to plan a specific behavioral reaction depending on the social context (Figure 3).

According to this 'social affordance' hypothesis (Box 1), the contributions of the parietal and premotor cortex to the planning of behavioral responses to the observed actions of others in social contexts are complementary, as previously established for graspable objects. Area AIP specifies observed action classes (e.g., manipulative actions) up to the level of exemplar (e.g., grasping), encoding their identity despite their continuous changes in the observer's retinal image [31,33].

Key Figure

The 'Social Affordance Hypothesis'
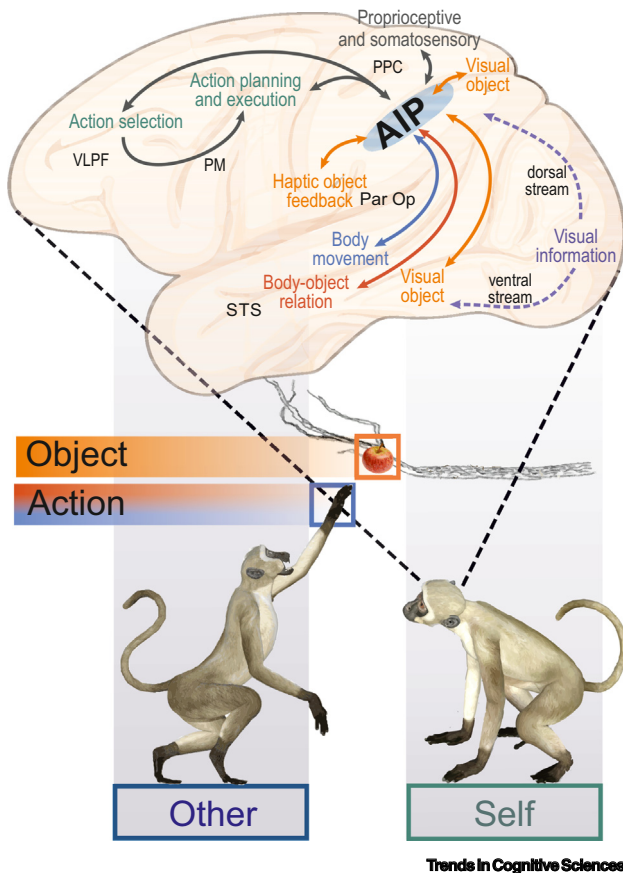

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Figure 3. The schematic representation illustrates the possible integration of OMA identity into the overall AIP motor function. Converging afferences reach area AIP from the anterior STS (vision of hand–object interaction), the middle STS (vision of others' body movements), and parietal/opercular (Par Op) cortices (haptic feedback from one's own object manipulation). Information about object shape, size, and texture reaches AIP from more caudal parietal regions and areas of the ventral stream; information about motion derives from visual areas of the dorsal and ventral visual stream. The integration of this information leads to the emergence of the visuomotor representation of others' actions that, as previously suggested for objects [47,51], can guide the selection and planning of the observer's potential motor actions in response to other agents, depending on the current context. Blue lines: visual signals about the other's body movement; red lines: visual signals about object features; grey lines: pathways for one's own action execution; orange lines: haptic and visual information about object. Strong connections with adjacent inferior parietal, superior parietal, and intraparietal areas (add rich somatosensory input about one's own actions to the haptic feedback coming from parietal operculum (orange line). Abbreviations: AIP, anterior intraparietal area; OMA, observed manipulative actions; Par Op, parietal operculum; PM, premotor cortex; PPC, posterior parietal cortex; STS, superior temporal sulcus; VLPF, ventrolateral prefrontal cortex.

In turn, the visual identity of observed actions is linked with a variety of potential motor plans, which are further selected and continuously updated in the frontal motor system, where they can finally be turned into a behavioral response appropriate to the other's observed action, depending on the current context and subject's goals. In this respect, prefrontal input to AIP [30,36] and its projections to territories of the putamen targeted by premotor and prefrontal hand-related fields [52], may play a critical role in the selection of the most appropriate behavioral response to a given

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Box 1. Extending the Concept of Affordances

The concept of affordances refers to the action possibilities of the environment that are available to an animal: 'the affordances of the environment are what it offers the animal, what it provides or furnishes, either for good or ill' [13]. Gibson introduced this concept to overcome the classical dichotomy between perception and action, but most of extant studies have exclusively focused on the investigation of object affordances [51,90–94].

Notably, the classical concept of canonical neuron [95], that is, a cell with pure object-specific selectivity during both the viewing and grasping of an object, was challenged by findings that single-neuron selectivity for an observed object rarely exhibits a one-to-one match with its motor selectivity during object grasping [20,48]. In fact, it has been shown that during visually-guided action planning, anterior intraparietal area (AIP) neuronal populations (rather than single cells) extracts visual features of a variety of objects and encode them in a neural space that emphasizes the visual similarity between objects' features, while the premotor cortex turns the parietal signals into a motor format, emphasizing the similarity of the motor plans required for grasping them [20]. These findings elegantly showed how object affordances compete to be turned into actions [51,90].

Nevertheless, in addition to inanimate objects, other agents and their behaviors constitute extremely relevant elements of the environment because they offer a variety of action and interaction possibilities. It is well established that others' actions, likewise graspable objects, are often encoded in a space-constrained manner in a variety of cortical areas [48,96–100], suggesting that motor plans in an observer's brain can be automatically recruited not only by observed objects but also by observed actions. Indeed, AIP neuronal populations group together in the neural space of the observed manipulative actions (OMAs) with maximally similar hand-object dynamic relationships [31]. Contextual situations may strongly influence what action is most appropriate as a response to an observed one; accordingly, AIP neurons with visual selectivity for observed grasping do not show more frequent or stronger motor responses during grasping than neurons with visual selectivity for OMAs, other than grasping [30]. These findings suggest that a variety of OMAs can afford the observer's 'grasping' as a suitable motor response and, we hypothesize, even a larger variety of alternative motor actions beyond grasping in other territories of the parietal cortex, suggesting that 'social' affordances exist alongside 'object' affordances.

OMA. Thus, we propose that, by means of facilitated OMA-selective neurons, specific OMAs are mapped on the neural substrates for action planning. This neuronal population works in parallel with, and to some degree may even overlap, the neuronal population encoding objects' physical features. On the other hand, suppressed OMA-selective neurons, which discharge only during grasping in the light and therefore lack any genuine motor response, may provide visual feedback about goal attainment with one's own action, thereby contributing to differentiating the visual signals related to the self (see also [22]) from those related to others.

Indirect evidence supports the notion of a praxic role for OMAs in phAIP as well [33]. Indeed, although human patients are paralyzed and cannot actively move, single-neuron recordings have provided evidence of imagery-related activity in the human anterior intraparietal cortex [53]. Furthermore, accumulating evidence has strongly demonstrated that neural activity along the human rostral intraparietal sulcus plays a causal role in controlling hand shaping during grasping [54,55], likewise in the monkey AIP [49], even with possible direct access to the primary motor cortex in both humans [56–58] and monkeys [59,60]. In addition to its well-established motor role, phAIP may have acquired a greater relevance in human perceptual functions [61–63], a relevance not clearly established for monkey AIP [19]. In particular, the relative view invariance of OMA-selective neurons reported in phAIP [33] is consistent with the evidence that healthy human subjects can discriminate observed actions in a largely view-independent manner [35]. Moreover, in functional magnetic resonance imaging (fMRI) experiments requiring OMA discrimination, phAIP exhibits increased activation relative to control conditions [64]. Thus, featural attention to OMAs may increase the gain of neuronal tuning curves in phAIP, as previously demonstrated for attention to motion direction in macaque medio-temporal neurons [65]. Furthermore, OMA-selective neurons in phAIP may contribute to cognitive functions beyond perception, such as a semantic role during the reading of action verbs [33] and a cognitive function in the encoding of the numerosity of observed actions [66], which may further support social interactions in highly complex, uniquely human situations.

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Action Classes beyond Manipulative Actions

So far, we focused on manipulative actions, which is by far the most widely investigated action class. But the behavioral repertoire of both human and non-human primates is much larger and more extensively articulated (Box 2). Thus, it is reasonable to hypothesize that dedicated 'visuomotor modules' [67] exist in the posterior parietal cortex (PPC) [28,68] and underlie the planning of a variety of action classes, following the principles we have outlined for OMAs in AIP. Although single-neuron evidence of action observation activity in other parietal regions of the monkey is scarce [26], indirect evidence from noninvasive human studies supports this hypothesis [64,69–71]. To conclusively test this model, however, more extensive studies that include a variety of action exemplars articulated in a larger set of classes are needed. Our prediction is that each PPC region devoted to the visual processing of a given action class will follow the blueprint for OMA-identity coding in AIP (Figure 3), thereby depending on two main types of visual signals to compute the identity of observed exemplars: the first concerns others' body movements and the second the effects of such movements on the outside world, including inanimate objects, other individuals, and the relationship between the actor's body and the environment.

The first type of visual signals should originate, for most action classes, from the middle STS (areas IPa/PGa) or its human homologue, and specify the dynamic changes of other's body parts [15], such as during reaching with the arm or walking. Indeed, the middle STS region is connected with most PPC regions, both directly (to the inferior parietal lobule) and indirectly (via inferior parietal regions that project to superior parietal ones) [37,72,73].

The second type of signals may arise from various regions of the visual system, depending on the action class, and they specify the effects of actions on the environment. For example, the actor's body motion in space (e.g., during locomotion or climbing) can benefit from afferents from the medio-temporal complex [43,74,75] as well as from the contribution of other visual motion brain regions [76], including the V6 complex [77,78]; the spatial relationship between an effector (e.g., the hand or mouth/face) and the target (e.g., during reach targets in 3D, manipulation, or self-directed actions) can be conveyed by projections from the rostral STS [23] or its human homologue posterior occipitotemporal sulcus. Finally, it cannot be excluded that both signals reach the parietal cortex through prefrontal projections, particularly from area 46, which is linked with both the regions signaling body movements and action effects on objects and the environment [79,80].

Taken together, these findings support the idea that action classes are a plausible, although still largely unexplored, interpretational framework that may apply to large sectors of the PPC, where the encoding of action identity demonstrated thus far for manipulative actions in the human and monkey AIP can apply to a larger variety of action classes to support action specification and selection in social contexts.

Concluding Remarks

Visual identity coding is the endpoint of visual processing [9,81]. Here, we have proposed that the computation of OMA identity in the dorsal pathway can lead to praxic functions, that is, the planning of behavioral responses during interactions with others. We have provided data supporting a model in which the manipulative action of others, in both humans [33] and monkeys [31], represents social affordances, conceived as the variety of action possibilities offered to an individual by other agents' behaviors. Thus, the notion of affordance competition [51] should be extended from the realm of inanimate objects to that of others' actions. We have shown that AIP appears to play a crucial role in this function for manipulative actions but have also hypothesized that this framework can apply to the larger variety of action classes in the primates' behavioral

Outstanding Questions

What is the relative contribution of suppressed OMA-selective neurons, identified in both the human phAIP and the monkey AIP, relative to that of facilitated neurons? And why are they suppressed in phAIP during silent verb reading also?

What are the neural mechanisms by which the brain can achieves a stable readout of others' bodily actions beyond manual actions?

What would a neurobiologically plausible articulation in action classes of the large human behavioral repertoire of bodily actions look like? Is it feasible to achieve a data-driven clustering of these classes?

How are observed bodily actions of others mapped onto motor plans of one's own actions? In other words, what is the visual-to-motor correspondence when bodily action classes are mapped in other brain regions beyond the parietal cortex?

How are social affordances processed in multiple and variable social contexts?

Will it ever be possible to efficiently decode bodily-action classes of self and others and to discriminate specific actions from the population activity of the parietal cortex (or any other brain region) during unconstrained social interactions?

Box 2. Action Classes

Action classes represent the highest level of categorization of observed actions, as previously proposed for objects [101,102]. Action exemplars within a class share the same general motor goal (e.g., changing the form or position of an object, moving the body in space, or influencing another's behavior); furthermore, the goal is typically achieved with an effector (e.g., forelimb, leg, or mouth) or a coordinated set of effectors (e.g., hand and mouth) that cause a change in the relationship between the agent's body and the objects, substrates, or conspecifics.

Strong neuroscientific support for the existence of 'action classes' has come from intracortical microstimulation studies in the macaques, using trains of pulses long enough to approximate the duration of ethologically-relevant actions [103]. These studies have revealed the existence of at least eight action classes, mapped along the dorsoventral extent of the frontal premotor cortex and linked to specific sectors of the personal and peripersonal space: (i) climbing/leaping, (ii) reach-to-grasp, (iii) hand-to-mouth, (iv) face/arm defensive actions, (v) gaze shifts, (vi) manipulative actions, (vii) hand in lower space, and (viii) mouth actions (chewing/licking). Similar results have been obtained from investigations of the parietal cortex of the prosimian galagos [2], with a dorsoventral arrangement along the lateral parietal surface with functionally matched domains in anatomically linked sectors of the premotor and motor cortex: hindlimbs, forelimbs, face, and eyes. Taken together, these findings show that phylogenetically ancient, parallel fronto-parietal circuits in primates support ethologically relevant action categories [104], which can be more finely controlled and displayed when naturally performed by the animals in their environment [105].

From a comparative perspective, the human behavioral repertoire is even larger than that of non-human primates. Electrical stimulation studies in human patients have, on one hand, confirmed the possibility of evoking mostly complex movements [106], sometimes with evidence of 'actotopic' organization [107]; on the other hand, they lack the details of monkey intracortical microstimulation studies. A more detailed, data-driven mapping of action-class topography in humans has been achieved in the observation domain. Indeed, fMRI studies showed that parts of the human posterior parietal cortex (PPC) exhibit selectivity for observed-action classes, such as manipulation, locomotion or climbing [69–71].

Based on the findings reviewed previously, we tabulate a non-exhaustive list of putative action classes. This list provides a more concrete frame for our theoretical proposal and can be used to guide future studies on action representation and the neural bases of visually guided social interaction.

Table I. List of Putative Action Classes, their Motor Goal, Typical Effector(s), and Prototypical Exemplars

Action class[a]	General motor goal	Effector/s[b]	Prototypical exemplars	Refs
Manipulation	Change form or position of small objects	Hand/fingers	Bring, drag, grasp	[31,33,64,69,108]
Reach targets in 3D	Attain target in 3D	Arm/eye	Gaze, point, reach	[109,110]
Defensive	Avoid target in 3D	Whole body	Blink, duck, parry	[103]
Self-directed	Change state of own body	Hand	Groom, rub, scratch	[70]
Gestures	Send a signal/modulate others' behavior	Face and trunk	Staring, threatening, lip-smacking	[111]
Ingestion	Ingest food	Mouth and throat	Chew, lick, swallow	[71]
Interpersonal	Modulate others' behavior	Whole body	Aggression, chase, courtship	[70]
Vocal communication	Modulate others' behavior	Vocal tract/mouth	Call, grunt, shout	[71]
Locomotion	Move own body in 2 or 3D	Legs and arms	Walk, crawl, climb	[69,76,112]

[a]We considered only natural action classes shared by human and non-human primates; that is, we did not consider actions performed with tools or highly symbolic or linguistic communicative actions. Several of the classes therefore have remarkable similarities to the categories described by the intracortical microstimulation studies mentioned previously, and it is plausible to consider them readouts from the neural activity of parieto-frontal cortical regions of freely behaving primates.
[b]A typical effector (e.g., the hand for grasping) can be flexibly replaced by another (e.g., the foot or mouth) in particular circumstances [113].

repertoire. Importantly, recent simultaneous recordings from multiple areas in animal models and the application of dynamical system frameworks to the analysis of neuronal populations data [82,83] greatly contributed to elucidate the visuomotor transformations underlying the identification and selection of object features relevant for action planning and execution [20,84]; these approaches will likely play an important role in deciphering the neural and computational principles underlying social affordance processing in different contexts (see Outstanding Questions).

Single-neuron recordings in humans are a powerful tool for investigating the neuronal substrate of behavior. To overcome the limitations of studies of paralyzed human patients, who obviously cannot provide hints about the motor processes underlying action-identity coding, future studies should capitalize on the opportunity to record neurons from freely moving non-human primates. Such recordings would allow the sampling of neuronal activity in a sufficiently complex environment, which could be used to study a broader variety of action classes in the behavioral repertoire of monkeys; thus far, similar investigations have been carried out almost exclusively in rodents [85,86]. Thus, combined human and non-human primate investigations seem to be the most suitable approach to encompassing the neuronal and behavioral levels in a translationally relevant manner and to reconciling the necessity of the most appropriate animal model with the need to reduce and refine as much as possible the recourse to non-human primates for indispensable neuroscientific basic research [87].

The proposed approach would provide a firm neurophysiological and ethological basis for hypotheses that maintain that cortical motor neurons play a role in the integration of convergent sensory information regarding not only physical objects but also the observed bodily actions of others (see Outstanding Questions). Under such hypotheses, the observed other represents a rich source of social affordances for the self. The alteration of the mechanisms underlying social affordances processing can lead to devastating neuropsychiatric diseases [88,89], whose underlying neural bases are still poorly understood.

Declaration of Interests
No interests to declare.

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