

Neural systems underlying the prediction of complex events

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Abstract. Animals depend on predictions about the near future to react and act in a timely, situation-appropriate fashion. Prediction is particularly challenged in the face of events: these entail a stimulus whose temporally directed structure is meaningful in itself. Many simple events, e.g. regular motion, can be predicted by means of dynamic-forward extrapolation. For this class of predictions, the premotor-parietal network is active which we also need to plan our own body movements. However, when it comes to complex events such as action, speech, or music, we additionally need to retrieve semantic and episodic memories in order to feed and restrict the required predictions. These processes are reflected in activity of functionally specialized brain networks, as outlined in the present article for the case of action prediction. Here, knowledge about objects, rooms, and actors is exploited, but also action scripts that account for the actions' probabilistic architecture.

Keywords: Action observation, dynamic-forward extrapolation, probabilistic prediction, object knowledge, rooms, actor, action scripts, episodic memory, semantic memory, premotor cortex, inferior frontal gyrus

'Smiles, walks, dances, weddings, explosions, hiccups, hand-waves, arrivals and departures, births and deaths, thunder and lightning: the variety of the world seems to lie not only in the assortment of its ordinary citizens—animals and physical objects, and perhaps minds, sets, abstract particulars—but also in the sort of things that happen to or are performed by them.' [1]

'The fraction of an action is more than a movement.' [2]

1 PREDICTION IN COGNITIVE NEUROSCIENCE

Prediction, anticipation, expectation, and prospection are terms that describe some kind of mental orientation towards the future. Cognitive neuroscience is addressing how this mental orientations manifests in the brain. In principle, there are two phenomena that cognitive neuroscience is interested here: firstly, the manifestation of an energetic investment, i.e., an increase in activity reflecting that some source of infor-

mation in memory and/or in the environment are exploited in order to produce an estimate of the upcoming; and secondly, the manifestation of a benefit, i.e., a decrease in activity reflecting that some information provided by the environment does not have to be awaited or fully processed because it already has been estimated or deduced from other sources of information. As will be outlined in this paper, the networks where these two effects can be measured may sometimes overlap, but mostly they are fully dissociated. Many studies in prediction use expectation violation paradigms: showing that the unexpected event corresponds to an increase of brain activity is taken as an indirect evidence for the preparation that has occurred beforehand.

Historically, the notion of a predictive brain has been propelled by Helmholtz' proposal of efference copies cancelling self-induced sensations during saccades [3]. Travelling faster than the efferent signal itself, they were taken to stabilize head-centred representations of object locations. This notion has been incorporated, generalized and further developed in modern concepts on how animals tune and optimize their body movements, particularly motor control theory [4] and predictive coding [5,6,7]. Cognitive neuroscience is nowadays concerned with prediction in all classical domains, including action, perception, and cognition [8,9].

Hardly surprising, there is a confusing multitude of factors to specify the very nature of predictive phenomena across different contexts: Predictions are deemed probabilistic or deterministic, they are highly or sparsely specified, can be explicit or implicit, and they occur on very short to very long timescales [10]. Against this backdrop, there has as yet been no success to provide a systematic account of predictive mechanisms, neither behaviourally nor with respect to the brain, although there are recent efforts to do so [8]. The present paper addresses the neural basis of prediction of complex perceptual events and the peculiarity thereof.

2 'EVENT' IN 'EVENT PREDICTION'

When we expect, for instance, the bang of a detonation while observing a blasting operation, we expect a sensory state happening at a certain point of time, e.g. after an acoustic warning signal. Although one may say that the detonation bang is an event that occurs, the term 'event perception' or 'event prediction' is used to refer more specifically to the transformation or metamorphosis of some present stimulus that continuously evolves in spacetime. This entails that some parts of the upcoming stimulus are already there in the presence and remain unchanged while the event takes place, such as for instance the ball remains the same when being kicked and undergoing a trajectory.

Taking trajectories as a starting point, event prediction can come in two forms: either as a dynamic-forward extrapolation from current states and changes; or as a probabilistic estimation based on a number of previous samplings. Both kinds of prediction may be combined. For instance, when we observe the ball, its present position and the direction and velocity of its motion are considered when engaging a dynamic-forward

kind of prediction; alternatively, when we seek to estimate its landing point without tracking the ball during motion, a probabilistic approach of prediction seems more appropriate. For many events that we face in reality, we get along quite well with a combination of dynamic-forward and probabilistic sampling-based predictions.

However, there are further sources of information that shape our predictions, based on facts and factors that are learned and stored as our associative, episodic, or semantic memories. To stay with our example, even before the ball is kicked, we predict the ball to rise in an arc-shaped fashion and to return to ground because we have learned that balls do so in our world.

While the role of semantic knowledge is limited when we predict ball behaviour, it becomes highly relevant when it comes to human behaviour, particularly language and action. Prediction of these kinds of events can be considered being complex in the sense that they entail several layers of predictions and are most probably fed by several memory systems. At least, prediction of human action draws on the observer's script knowledge, but also often includes retrieval of episodic associations and social rules.

In the following, I will first turn to dynamic-forward kinds of prediction and their typical premotor-parietal network. Thereafter, some studies are reported addressing the factors that drive prediction of human action. They yield a neural basis that goes beyond the premotor-parietal network, reflecting the requirement to further fan out, feed and restrict prediction in the face of semantically loaded events such as action.

3 DYNAMIC-FORWARD PREDICTION

We developed the so-called serial prediction task to investigate explicitly instructed prediction of highly controlled visual or auditory stimulus sequences. It consists of stimulus sequences that are regularly structured – and hence predictable - with regard to one stimulus property, for instance size, colour or location. Participants are asked to attend to this property and to indicate in a dual choice response mode whether the regular structure was maintained until the end of the sequence or not. In the latter case, switching the presentation order of the last stimuli of the sequence violates its regular structure.

Studies show that serial prediction, as contrasted to serial match to sample, target detection, or n-back tasks, draws on the lateral premotor cortex and its corresponding projection sites in the lateral parietal cortex (for overviews, see [11,12]). These cortical areas are organised in multiple parallel and largely segregated loops and known to subserve sensorimotor transformation, that is tuning voluntary body posture and movement to environmental conditions and vice versa [13]. How could this specific sensorimotor function be reconciled with the same areas' role in serial prediction? One way is to adopt the notion of action as being planned and controlled by the action's anticipated sensory consequences or re-aferences (for a review of this so-called ideomotor theory, see [14]). Generalizing this predictive account from motor control

to perception, it has been proposed that premotor-parietal loops serve not only the prediction of self-induced sensory change but also the prediction of externally induced sensory change – in other words, events [15]. Note that the term "event" is meant to refer to the above-proposed definition – change that can be extrapolated from current state and changes - and that the prediction mediated by the lateral premotor-parietal network is meant to be dynamic-forward extrapolation. Thus, the particular quality of premotor-driven prediction is in the spatiotemporal reality (or *situat- edness*) of the transforming body or object that constrains its possible behaviours.

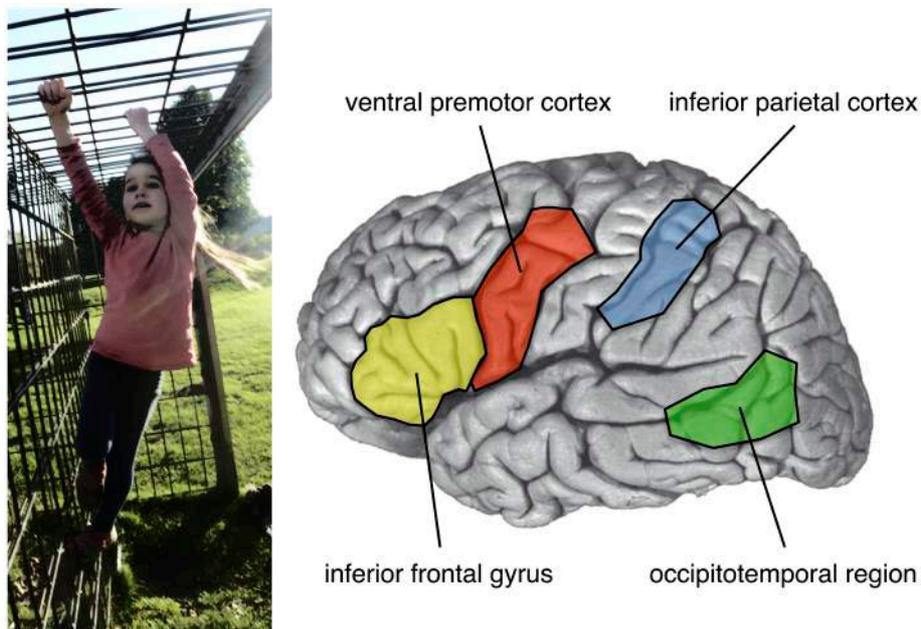


Fig. 1. Human action entails transformation that can be predicted in a dynamic-forward manner, but also transitions whose prediction requires the retrieval of semantic and episodic memories.

The former draws on premotor-parietal networks, whereas the latter additionally engages a multitude of prefrontal and occipito-temporal areas, some of which are depicted here.

4 PREDICTION OF OBSERVED ACTION

When we witness an action, a dynamic-forward kind of prediction is up to the transformation that an observed body and/or manipulated objects undergo. Hence, premotor-parietal loops can take on prediction up to this level of complexity. It can be shown that the lateral premotor cortex contributes specifically to the prediction of

upcoming action stages as compared to memorizing current action stages [16,17]. Recently it showed that premotor activity varies as a function of the selection among possibly upcoming object manipulations, whereas parietal and occipitotemporal cortex were reflecting the number of possible manipulations that a given object is associated with [18]. These findings are well in line with theories on the premotor-parietal interaction during action control [19]. They suggest that premotor cortex master a repertoire of transformation operations changing the body and/or object to specified end-states.

However, action is often more complex than a single object-directed manipulation of movement [20] and when action observation is compared to serial prediction, it shows that both share premotor-parietal loops, but action observation draws on additional sites in the brain [21]. Actually, four areas make up the typical 'action observation network' that has been found in most of the numerous studies in this field: in addition to lateral premotor and parietal cortex, it includes the inferior frontal gyrus (BA 44, 45, and/or 47) and the boundary between lateral temporal and occipital lobe shortly called occipitotemporal cortex. However, depending on the particular experimental paradigm and the addressed research question, still more brain areas can be found to be active during action observation. Obviously, human action bears large amounts of informational detail that draw on our memory systems, which in turn can be supposed to generate expectations on the upcoming action and to adapt and restrict these expectations to the actually observed action course. Yet, we are largely ignorant about what information action observers read out from the scene, and whether memories that may aid prediction are retrieved and shaped on the basis of these cues. Recent attempts to address some of these issues will be reported in the following.

4.1. OBJECTS, ROOMS AND ACTORS AS (PREDICTIVE) CUES

It is plausible to assume that taking into account what actions the manipulated object is frequently involved in, and where the action takes place, should improve action prediction. Or should we rather say: action *recognition*? One has to be cautious with claiming that certain neurophysiological effects are reflecting predictive but not retrodictive computations in the brain. As will be detailed below, we found that object-implied actions as well as room-implied actions have an effect on brain activity in action observers. We also know that object and room stimuli are processed much faster than manipulation stimuli, presumably because the latter are temporally extended (event-like) and disambiguate only over time. Therefore, finding that object-implied and room-implied actions modulate brain activity in action observers seems to support the idea that prediction is shaped by stimulus-cued semantic memories. However, these studies cannot settle whether the reported effects are really due to predictive or rather due to retrodictive processes - they merely show which cues are spontaneously considered in action scenes, not more. Still, this is an important step on our way to understanding the factors that may be relevant for human action prediction.

Neuroimaging data imply that even before manipulation of an object is shown, the mere presentation of this object triggers associated actions in memory, which in turn can impact action recognition [18]. Similarly, also the room wherein an action takes place is associated with a set of actions that are typically (frequently) observed therein, and data show that we spontaneously retrieve this information during action observation. For instance, when actions are shown in incompatible rooms as compared to either compatible or neutral contexts, activity increases in the inferior frontal gyrus [22]. When using pixelation to mask the manipulated object while preserving manipulation information for the observer, the same effect is observed, thereby ensuring that the effect is due to a conflict between the incompatible room and the presented manipulation, not between room and object. Under the same object-masking conditions, it shows that action-incompatible rooms slow down action recognition, whereas compatible rooms enhance correct recognition rates [23]. Finally, we found that already children at the age of four exploit contextual information during action recognition [24]. Here, it interestingly shows that compatible room settings are particularly beneficial for action recognition when experience with the presented action is sparse.

Together, these findings indicate that both object as well as room information are used during action observation to shape action recognition. As objects are associated with certain actions, and rooms are as well, one may speculate about a cascade of perceptual and retrieval processes that use object and room information to shape memory retrieval of associated and hence expectable actions. Competition, interactions and dependencies between these sources of information remain to be empirically investigated in detail. First studies reveal a fundamental cross talk between context, object and manipulation during action observation [25].

Beyond room and object information, action entails an actor or actress. We found that even when the actor or actress is task-irrelevant for the subjects, and attention to the actor or actress is hampered by a limited time window when focusing on identification of the presented action video, the identity of the actor or actress can have considerable effects on the neural processes of the observer. For instance, the observer's brain clearly registers whether the action takes place from the first or from the third person perspective (the latter being indicative of the presence of another one); whether the face of the actor or actress is visible or not; and whether the actor or actress is the same or a different as compared to the preceding action video [26]. Moreover, previous encounters with the same actor or actress trigger the attempt to integrate all actions of this actor or actress under one overarching goal, even if implausible [27]. Thus, re-encountering an actor or actress after a sub-minute delay, provokes a reference of his or her current action to those we saw him or her performing before.

Above reported findings indicate that objects, rooms and actors serve as cues that trigger expectation for certain actions. This is true in two respects. On the one hand, rooms and objects themselves imply which actions are typically associated with them. On the other hand, re-encountering an object, actor or actress triggers the expectation that the previously associated goal is now continued. The latter finding points to the activation of a script memory. These scripts enable embedding the current perception

into a larger temporal and semantic frame that can be used to both build predictions and restrict interpretations.

4.2 SCRIPT KNOWLEDGE

In a series of recent studies, we addressed the role of the inferior frontal gyrus in action observation. We here resort to the concept that the inferior frontal gyrus aids semantic and episodic retrieval by shaping stimulus-derived associative memories and selecting among retrieved associations [28]. Our working hypothesis is that this region's role in action observation is to retrieve action scripts the currently observed act fits into, thereby building the basis for predictions on upcoming action steps.

A script is meant to refer to a temporally structured sequence of acts ruled by the achievement of an overarching goal [29]. Formally, script memory is a sub-category of semantic memory, i.e. generalized knowledge about objects, facts and events, including their particular properties and systematic relationships to other objects, facts and events. Still, scripts are peculiar as they mostly consist of prototypical or generalized episodes and are intrinsically event-like. The term 'structured event complexes' coined by Grafman may account for this particular profile of knowledge format [30].

We found evidence favouring that during action observation, the brain spontaneously generates predictions on upcoming action steps by retrieving script knowledge, and that these processes are specifically reflected by an increase of activity in the inferior frontal gyrus. We argue that this search occurs spontaneously, as subjects were neither instructed to prepare for upcoming actions nor did this preparation improve the performance of their task to recognize actions in an unspeeded, retrograde manner. Activity in left inferior frontal gyrus transiently increases when the goal changes from one action video to the next [31]. This effect is specific for goal switching, i.e. it does not show up for object switches. The same area parametrically decreased during the unfolding of episodes with a coherent overarching goal [32]. Correspondingly, activity in this area increased during the unfolding of episodes that were incoherent with regard to their goals, but only when they were coherent with regard to the actor [27]. This finding indicates that the actor may serve as a trigger to search for an overarching goal. In yet another study, activity of bilateral inferior frontal gyri co-varied positively with the quantified level of goal coherence of two consecutive actions [33]. Interestingly, this latter effect depended on whether the two actions shared a common object, indicating, as in [31] and similarly as for the shared actor, that this object served as a trigger to search for an overarching goal.

Together, these findings suggest that objects, rooms and actors effectively trigger the memory of actions that we associate with them. These can be either retrieved from long-term semantic (particularly script) memory, or from previously encountered actions to which the current action seems to be linked by virtue of these cues.

4.3 USING STOCHASTIC STRUCTURES IN ACTION SEQUENCES

Human (or animal) prediction is stochastic, not deterministic; i.e., we engage in probabilistic estimations against the backdrop of our short- and long-term knowledge. Based on a history of probabilistically distributed events, we acquire knowledge about their general (or absolute) probability, but also knowledge about their conditioned (or relative) probabilities given certain contexts and/or preceding events. For instance, the overall probability of thunder is quite low, whereas it is very high after lightening. A straightforward assumption therefore is that when we engage in prediction of events, we should exploit statistical knowledge about the world, as this is the best that we have. Following the currently much-noticed predictive coding account, perception can be generally understood as Bayesian inference process [34]. While this conception has been spelled out for stimuli whose basic properties remain largely invariant across the range of seconds such as objects, prediction seems even more required when we face events. That is because, events consist not only of a contingent sequence of perceptual states, but their informational core, i.e., their *meaning*, originates from the particular temporal and probabilistic structure between these states.

To an observer, actions provide an ongoing stream of sensory stimulation. Still, observers are quite sensitive to the segments of actions and their probabilistic relationships [35,36]. We found that these segments or fractions of actions are not simply movements of the observed actor or the manipulated objects. Thus, when observers segment videos showing tai-chi sequences or actions, only the latter engage a complex network of prefrontal, parietal and parahippocampal areas when the stream passes a segment boundary [20]. Thus, actions are not simply perceived as modulations of the actor's movement kinematics (which is true for both tai chi and action videos, as indicated by increase in motion-sensitive area MT), but amount to meaningful action steps that trigger complex re-orientation processes propelled by retrieval from long-term memory of action scripts.

What now about the probability structures among consecutive action steps? As defined in the beginning, a script is here meant to be a temporally structured sequence of acts ruled by the achievement of an overarching goal. Depending on the particular situation and many other factors, one and the same script can consist of different sequences of acts, all effective to achieve one and the same goal. For instance, when you visit a restaurant, the first step when entering the restaurant can either be searching for a free table, or rather waiting to be seated by the restaurant's staff. Knowledge about the particular restaurant's policies, or certain external cues such as the presence of a desk near the restaurant's entrance, help us to select the appropriate action step. Actions are made of such probabilistic 'decision trees', and observers seem to apply this knowledge to the actions performed by others.

In experimental settings one seeks to control the quantifiable probabilistic structure of the actions the participant is presented with. In our studies, we therefore train subjects by iterative presentations of action sequences that feature fixed transition probabilities between consecutive action steps. After training, subjects enter the fMRI experiment where they encounter the same sequences again. Here we can investigate what structures co-vary with either the predictedness (level of surprise) of a given action and its

predictability (level of entropy). Both predictedness and predictability quantify corresponding brain responses, indicating that the brain engages in probabilistically tuned prediction, even when not required by the current task [37]. Recent unpublished data indicate that humans consider even the 2nd level of statistical structure in action sequences, i.e. the action preceding the preceding action, especially when the predictive information provided by the preceding action is low. Note that none of these studies required subjects to report or register probabilistic structures in actions, suggesting that measured effects reflect spontaneous and ecologically valid processes of prediction.

The violation of prediction based on conditioned or unconditioned event probability is considered being an indirect evidence for default preparatory mechanisms in perception. There is a unique surprise related to the first encounter with an unexpected course of a given action, and this surprise is typically followed by a slower learning process that needs several iterations of the new action course during which the involved cortical areas adapt to the novel script. For instance, when subjects were implicitly trained by action videos, and these actions were later repeatedly presented in a slightly modified version, we found a parametric attenuation in the action observation network mentioned above. This network hence showed to be sensitive to violations of predicted action courses and slowly adapted to the new script [38]. Interestingly, areas of the frontomedian wall (BA 10 and adjacent anterior cingulate cortex) also reflected the amount of bias between the two alternatives of a given action script. That is, when the number of video presentation times led to a bias such that one of the two alternatives had a higher predictive capacity than the other, activity increased in these areas. Based on the literature, we suggested that these biased states entailed a suppression of the weaker script version (see [38] for a detailed discussion).

Further studies corroborated the finding that areas of the frontomedian wall increase in activity when prediction has to be adapted. For instance, activity in dorsal frontomedian BA 8 was associated with the unexpectedness of observed actions, be they action errors or not [39]). Activity in the same cortical field was found to increase for actor movements that violated the observer's cued expectation [40]. In addition to frontomedian cortex, also caudate nucleus and the hippocampal formation (both particularly connected to the prefrontal cortex) are tuned to the violation of prediction and subsequent learning processes [40,41]. Based on these findings, we have argued that caudate nucleus, which is established as a carrier of reward-related prediction errors, may contribute more generally in signaling for prediction errors, not only when reward-related.

5 CONCLUDING REMARKS

The current paper aimed at giving a short introduction into prediction of complex events and our attempts to elucidate its presumed neural basis. Predictions as dynamic-forward extrapolation from current states and changes builds a basic but limited capacity to estimate how bodies and objects will change with regard to certain properties such as their location, speed, colour, pitch and so on. In contrast, the prediction of

action additionally requires the exploration and exploitation of a rich body of semantic and episodic knowledge associated with the action in its particular context, including at least objects, rooms, actors, and the action scripts embedding them.

We think that our findings provide a new view on the action-observing brain – a brain that is exploiting and exploring a huge number of informational details even when not required to do so. It is an open question why the brain invests so much energy to tap and integrate all these informational sources (Notably, most of these processes occur without the participant's explicit awareness or drive). It seems as if the brain does not care a lot for the cost-benefit ratio when investing resources in prediction. One obvious explanation is that current predictive profit is maximized. A slightly different explanation could be that this enormous effort is made in order to improve our knowledge (or 'internal models') about the world and thereby to become better predictors in future. According to this notion, there is always a certain surplus of information considered, simply in order to learn and train for new situations.

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