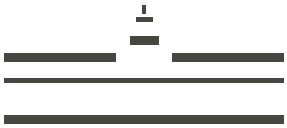

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# Neural Signatures of Statistical Structure in Observed Actions

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## Abstract

Humans have the intriguing capacity to accurately predict other persons' actions. However, how humans accomplish accurate predictions despite the large number of possible actions remains unclear. Everyday actions can be characterized by a statistical structure, so that knowing a previously completed action allows predicting likely next actions. The present thesis investigated whether human observers take statistical structures into account when generating predictions of observed actions. Three experiments using functional magnetic resonance imaging (fMRI) were conducted to test whether 1) different aspects of a statistical structure have distinguishable effects on the neural processing of observed action steps, 2) humans efficiently exploit additional information from a higher-order statistical structure in order to improve their predictions, and 3) whether humans are sensitive towards a hierarchical structure covering successive action steps that allows to group action steps into events. In all experiments, participants were presented with videos of sequences of action steps that followed pre-defined statistical structures. Participants gained implicit knowledge of these structures through passive viewing of the videos in separate training sessions.

The first experiment tested whether an action step's probability and predictability could be distinguished with regard to their effect on the action's neural processing. To that end, the probability of a certain action step following the immediately previous action was manipulated. Degrees of predictability were manipulated by expanding concurrent possibilities of action steps. As hypothesized, probability and predictability showed distinguishable effects on the neural processing of an action. Actions with low probability elicited a higher activation in the intraparietal sulcus, indicating higher processing costs associated with less expected action steps. Low predictability of upcoming actions led to increased activation across a fronto-parietotemporal network. This finding supports the

idea that humans integrate more information from their observations to account for low predictability.

The second experiment followed up on this observation. I tested whether exploitation of statistical structure follows an efficiency criterion. I hypothesized that human observers exploit additional information on an upcoming action step from the penultimate action step if predictability based on the directly preceding action step alone was insufficient. This would suggest a cost-benefit trade-off in the generation of predictions. The implemented statistical structure underlying action steps allowed distinguishing effects of information derived from only the last action step ($1^{st}$-order information) and of information derived from the combination of the last and penultimate action step ($2^{nd}$-order information). Findings showed that humans use both $1^{st}$- and $2^{nd}$-order information to predict upcoming actions. Activation in the rostrolateral prefrontal cortex was specifically modulated by $2^{nd}$-order information if $1^{st}$-order information was low. This supports the hypothesis of a cost-benefit trade-off in the use of information and suggests that the rostrolateral prefrontal cortex balances the exploitation of information. Together, the first two experiments showed that human observers are sensitive towards sequential regularities among action steps and exploit information derived from these regularities in a cost-benefit sensitive manner.

In everyday actions, action steps are grouped into distinct events. To successfully predict upcoming action steps, it is necessary to take information on the current event into account and not only rely on preceding action steps. In the third experiment, I tested whether human observers use an event structure that emerges from associations among successive action steps to predict upcoming action steps. Surprisingly, neither functional nor behavioral data provided evidence for participants' use of the event structure or sequential regularities among action steps. Instead, an effect of an action step's frequency

in the recent past on activation in the intraparietal sulcus and posterior temporal regions was found *post hoc*. This possibly reflects a frugal mechanism to optimize processing of actions. I elaborate on possible reasons for participants' negligence of the statistical structure implemented in the third experiment and point out differences between the first two and the third study.

I discuss the results from the three studies with regard to their generalizability to everyday actions as well as their implications for our understanding of action prediction as a function of the action observation network.

# 1 Introduction

## 1.1 Understanding and predicting actions

A crucial ability for successful human behavior is our ability to understand and predict other peoples' actions. This allows us to efficiently interact with each other and work towards a common goal (Sebanz & Knoblich, 2009). But how do we come to understand and process others' actions?

Actions and their understanding bring about various challenges. Even simple actions[1] like preparing a cup of tea can be performed in many different ways or the same action can be interpreted differently depending on its context (Kilner, Friston, & Frith, 2007; Wurm & Schubotz, 2012). This ambiguity of actions gives rise to an inverse problem of action understanding (Csibra & Gergely, 2007). Moreover, actions develop over time. Thus, perception of the action changes constantly, which adds to the interpretation or recognition of the action. Actions can also be understood and described on different timescales or levels. There are at least four different levels (Kilner, 2011): 1) an action's *motor level*, i.e. the pattern of muscle activity, 2) action *kinematics* that compose an isolated movement, like moving one's arm, 3) the immediate *goal* of the action, like grasping a cup, and 4) the action's *intention* which reflects the mental state of the actor, e.g. to satisfy one's thirst (Kilner, 2011).

Importantly, the term *goal* itself is ambiguous and can be interpreted on different levels of abstraction. The most basal meaning of goal is the object or location an action is targeted at (Hamilton & Grafton, 2006). Another definition of goal is the desired end-state or outcome of an action, for instance, preparing tea (Csibra & Gergely, 2007). Notably,

[1] In the present thesis, the term *action* always refers to acts aiming to accomplish a certain end-state or outcome, in contrast to autotelic actions that could also be referred to as activities.

following this definition, multiple action steps and their associated sub-goals might be necessary in order to accomplish a goal (boiling water, pouring the water in a mug, and adding a tea bag). By spanning a sequence of action steps, this latter definition of goals forms an intermediate level between goals as implied in the taxonomy by Kilner (2011), and an action's intentional level, defined as an actor's believes and desires (de Lange, Spronk, Willems, Toni, & Bekkering, 2008). In the present thesis the term goal will always be used as an action's desired end-state.

Despite the complexities resulting from the different levels on which an action can be understood, humans can easily assign a goal to an observed action (Csibra & Gergely, 2007). Moreover, various lines of evidence support the notion that humans incidentally predict an observed action. For instance, humans are particularly quick and accurate at recognizing actions, even if visual information is sparse (Blake & Shiffrar, 2007) or parts of the action are occluded (W. Stadler et al., 2011; Zacks, Kurby, Eisenberg, & Haroutunian, 2011). In the following, I will give a brief overview of evidence for predictive processes during action observation before introducing early theories accounting for those capacities.

### 1.1.1 Empirical evidence for action prediction

The neural basis of understanding actions has been of longstanding interest in neuroscientific research, especially since the discovery of *mirror neurons* in the area F5 of the macaque cortex (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). These neurons have been found to fire not only when the macaque performs a particular action but also when the same action is only observed. This finding led to the proposal that mirror neurons might underlie the ability to understand actions (Rizzolatti, Fogassi, & Gallese, 2001). Predictive mirror neurons were recently identified to discharge ahead of the execution of a predicted movement (Maranesi, Livi, Fogassi,

Rizzolatti, & Bonini, 2014), corroborating the predictive nature of action observation. Although direct evidence for the existence of mirror neurons in the human brain is still lacking, as this requires single-cell recordings, these findings have influenced research on action observation in humans (Molenberghs, Cunnington, & Mattingley, 2012).

Early findings showed that observation, imagination, and execution of actions by humans activate a largely overlapping network of brain regions, among others composed of primary motor cortex, premotor cortex, and parietal cortex (Jeannerod, 2001). This observation led to the proposal that observers achieve action understanding by emulating an observed action using an internal model based in their own motor system (Grush, 2004). Critically, an internal emulation of an observed action does not need to be predictive. Therefore, these findings alone cannot be considered proof for the predictive nature of action observation.

More recent studies support the proposal of predictive processes during action observation. For instance, a rise of the *readiness potential*, which is an electrophysiological marker of motor preparation, can be observed before an expected action comes into effect (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004). Moreover, observing unexpected actions results in higher activation in a fronto-parietal network when compared to expected actions measured as the difference in the blood-oxygen-level dependent (BOLD) signal (Ondobaka, de Lange, Wittmann, Frith, & Bekkering, 2015). This activation was found to attenuate with repeated encounters of an action, possibly reflecting adaptation of action predictions based on experience (Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013).

Various sources of information, composing our action knowledge, can serve as basis for the prediction of an observed action. Identifying the influence of different aspects of action knowledge on action processing has gained increasing attention over the past years. First, in transitive actions, i.e. actions that involve a manipulation of an object, the

manipulated object already provides information on the upcoming action (Schubotz & von Cramon, 2008; Schubotz, Wurm, Wittmann, & von Cramon, 2014; Wurm, Cramon, & Schubotz, 2012). Research using transcranial magnetic stimulation (TMS) suggests that already seeing an object triggers the associated motor plan (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009; Cardellicchio, Sinigaglia, & Costantini, 2011), even if no execution is required. Information inherent to an object, like a possible manipulation, can also be used to predict actions of others (Bach, Nicholson, & Hudson, 2014). It could be shown that actions involving objects with many possible manipulations elicit a higher BOLD response in the so-called action observation network (AON), composed of premotor cortex, parietal and posterior temporal sites (Schubotz et al., 2014). This increased activation suggests the generation of a higher number of internal *forward models* of possible actions (see section 1.1.2).

Second, an action's spatial or temporal context can serve as basis for a prediction. Contextual influences on action recognition have been investigated in a series of experiments by Wurm and colleagues (Wurm et al., 2012; Wurm, Hrkać, Morikawa, & Schubotz, 2014; Wurm & Schubotz, 2012). The authors showed that actions are recognized quicker if they take place in a compatible context, e.g. kitchen actions taking place in a kitchen instead of an office (Wurm & Schubotz, 2012). They also found that incoherence between actions and context led to increased activation in the inferior frontal gyrus (IFG). Another study showed that activation of the IFG was attenuated when observed action steps formed a goal-coherent episode (Wurm et al., 2014). This suggests that humans use past observation, i.e. the action's temporal context, to make predictions of observed actions (Wurm et al., 2014). If the goal of an action is known, then the observer can predict the relevant further action steps that need to be executed to accomplish this goal (Csibra & Gergely, 2007).

This research shows that the human brain has the capacity to gather and reconcile information to predict upcoming actions based on action knowledge. However, how action knowledge is acquired in the first place and how the prediction is implemented neurally remains unanswered. One of the earliest theories regarding the neural mechanisms of action prediction is grounded in motor control theory, which will be explained next.

### 1.1.2 Internal forward models and motor control

The theory of an *efference copy model* developed by von Helmholtz (von Helmholtz, 1867) and further established by Sperry and von Holst and Mittelstaedt (Sperry, 1950; von Holst & Mittelstaedt, 1950) is one of the earliest theories assuming internal models of actions. The core assumption is that for every executed action an efference copy is generated allowing for a prediction of an action outcome based on a copy of the involved motor command. This efference copy is combined with the perceived sensation which allows for a better interpretation of the sensation's causes. This phenomenon can be explained using the example of object localization (Wolpert & Flanagan, 2001): To determine the location of an object in space, it is necessary to integrate the object's retinal location with the gaze position of the eye. This can be achieved through efference copies: rather than sensing the gaze position of the eye, the brain *predicts* the gaze position based on the action command that generated the eye movement, which is referred to as efference copy. Perceived motion of objects on the retina that is due to the eye movement is then cancelled out and the object's localization is perceived as stable. In contrast, if the eyeball is pushed from outside and thus forced into motion, no efference copy of its movement is generated. Accordingly, the motion pattern cannot be cancelled out from the visual perception, and the object is perceived as moving.

The idea of efference copies has been developed further by Wolpert and colleagues (Wolpert & Flanagan, 2001; Wolpert & Kawato, 1998) in the *motor control theory*. Motor control theory assumes the existence of two different models: an *internal forward model* and an *inverse model*. The forward model is assumed to be internal to the central nervous system and reflects the relationship between actions and their consequences. The sensory prediction derived from the forward model and the actual sensation are compared to each other. If they match, sensory effects are cancelled out. Thereby, sensations that result from self-motion are attenuated, whereas other, possibly more relevant sensory information gets enhanced (Wolpert & Flanagan, 2001). Using forward models to predict sensory consequences rather than sensory feedback allows for more accurate and quicker movements. Forward models are flexible and subject to experience and learning. This allows their adaptation to changes in the environment (Wolpert & Kawato, 1998).

Each forward model is paired with an inverse model (Wolpert & Kawato, 1998). The forward model contains a prediction of the next body state accounting for its current state and a motor command. Inverse models can act as controllers by providing the motor command that causes a desired change. In order to find the right motor command despite the present uncertainty in the environment, for instance when handling an unknown object, motor control theory proposes that the brain runs multiple forward models simultaneously (Wolpert & Kawato, 1998). The forward model whose predictions match best with the sensory feedback of the action is then selected, and the associated inverse model as controller of the subsequent motor commands is instantiated (Wolpert & Flanagan, 2001).

The theory has been supported by numerous findings on motor control and motor learning (Wolpert, Diedrichsen, & Flanagan, 2011) and provides explanations for a multitude of behavioral phenomena, e.g., the reduced perception of agency under temporal

displacement (Sato & Yasuda, 2005), grip adjustment to objects (Flanagan & Beltzner, 2000), or perceived intensity of self-applied stimulation (Blakemore, Wolpert, & Frith, 2000, 1998).

Intriguingly, Wolpert and Flanagan (2001) proposed that motor control theory could be extended to also account for predictions of events beyond self-controlled movements, for example, when observing others. In this situation a forward model is assumed to only predict possible sensory outcomes without the necessity to actually perform the action. However, the theory reaches its limits when trying to explain how we come to understand another person's goals or even intentions underlying an action. This is because the internal forward model is limited to an action's motor or kinematic level which are insufficient to understand and predict another person's action (Kilner, 2011). Additional information that is not inherent to the action itself but to the spatial or temporal context in which it appears needs to be taken into account, as this also affects processing of actions (cf. section 1.1.1). This relates to the so-called *one-to-many-mapping* (Kilner, 2011) which describes that depending on the context, actions that are the same on the kinematic level can be performed in order to reach different goals. A possible account for this problem will be presented in a later section.

## 1.2 Prediction as a core mechanism of the brain

While the previous section focused on prediction of actions, it has already been proposed from early phases of psychological research that all perception and cognition can be understood as predictive (see Bubic, von Cramon, & Schubotz, 2010, for a review). This idea is present in a broad spectrum of psychological research, for instance in theories of classical conditioning (Rescorla & Wagner, 1972), associative learning (Nissen & Bullemer, 1987), or optical illusions (O'Reilly, Jbabdi, & Behrens, 2012). Thus, prediction is not

limited to the motor system but rather a general property of the brain. This proposal has gained increasing attention over the past years of neuroscientific research in the framework of *predictive coding* (Clark, 2013).

### 1.2.1 Predictive coding

Within the framework of predictive coding, all sensory perception is considered as predictive. The core assumption of predictive coding is that the informational content of a sensation can be compressed if only the deviations from its prediction need to be processed (Clark, 2013). If the brain only processes unpredicted aspects of a stimulus, neural processing is metabolically more efficient. Thus, the main principle of neural processing is to optimize the internal model to most accurately predict current sensations. By this, predictive coding goes further than motor control theory as its assumptions are not limited to the motor system and action selection but claim to build the framework for global brain functioning (Friston, 2005).

Predictive coding is proposed to operate across different hierarchical levels of the brain (Friston, 2005; Lee & Mumford, 2003; Rao & Ballard, 1999). On each level, hypotheses about the causes of the current sensation, also referred to as *generative models*, are formed and fed back as predictions to lower levels of the processing hierarchy. If the prediction and the current sensation match well, the probability of the generative model rises, i.e., the model gets strengthened. However, if a mismatch, a so-called *prediction error*, is registered, this error is fed forward to the hierarchically higher levels and the generative model is adapted (Friston, 2005; Rao & Ballard, 1999). This process continues throughout all levels until the correct prediction about the sensation is found.

The predictions are proposed to be generated in a Bayesian fashion and are probabilistic in their nature (Friston, 2010). The generative model becomes part of lower

levels as a prior probability of a sensation's cause. Priors are compared with the sensory evidence and a posterior probability of the most likely cause can be derived. Which generative model is considered best to explain causes of sensation is also chosen in a Bayesian way, reflecting the most likely causes given a current context (Clark, 2013). The Bayesian property of predictive perception is supported by research showing that the uncertainty associated with a stimulus is reflected in the weight given to the sensory evidence compared to the weight given to the predictions based on the generative model (Clark, 2013; Fiser, Berkes, Orbán, & Lengyel, 2010; O'Reilly et al., 2012). In other words, if a stimulus is highly uncertain, for instance the perception of a word in a noisy environment, the interpretation of the stimulus is influenced more strongly by the prediction about the identity of the stimulus (Summerfield & de Lange, 2014).

Notably, predictions and prediction errors are assumed to engage separate sub-populations of neurons, so-called *representation* and *error units* (Friston, 2010; Rao & Ballard, 1999; Summerfield & Egner, 2009). While accurate predictions allow for "explaining away" the predicted signal associated with a sensation, the prediction itself is proposed to lead to an enhancement in the neural population of representation units (Friston, 2005).

In an extension of the theory of predictive coding, Friston and colleagues included actions, supposing that action and perception are implemented through the same functional mechanisms (Friston, 2010). According to Friston, perception and action work closely together in so-called *active inference*, which states that the brain not only searches for the best model to predict sensations but that actions can be initiated to actively seek or generate the predicted sensations. This account bears close resemblance with the proposed inverse model acting as a controller of future actions as put forward by Wolpert and colleagues (Wolpert & Flanagan, 2001; Wolpert & Kawato, 1998) in motor control theory (cf. section 1.1.2). In motor control theory, it is postulated that a controller is selected

based on its paired forward model's fit to the current sensations. The selected controller then determines future motor commands which match best with its predictions of the current action context (e.g., whether a full or empty box is picked up). Thus, as in active inference, motor commands are assumed to be initiated by a controller in order to minimize upcoming prediction error. While Wolpert and colleagues assume two separate internal models for this, Friston's theory of predictive coding and active inference relies on only one model and its inversion (Kilner et al., 2007), rendering Friston's theory simpler in its assumptions.

Predictive coding was intended to explain how the brain processes current sensations rather than how predictions about upcoming observations are made. However, from the premise of hierarchically higher predictions follows that those higher areas generate predictions over a time course of at least seconds (Hohwy, 2012), thus being potentially prospective. Consequently, the general principle of predictive coding, assuming that higher areas pass hypotheses about sensations to hierarchically lower areas, should be applicable to prediction in the case of action observation. This will be outlined in the next section.

### 1.2.2 Predictive coding in action observation

As mentioned previously (section 1.1.2), motor control theory aimed at explaining how humans come to predict other peoples' actions, and it was proposed that predicting others' and one's own actions engages the same mechanisms (Grush, 2004; Jeannerod, 2001; Wolpert & Flanagan, 2001). Actions can be described and understood on different hierarchical levels, i.e. on the *motor* level, the *kinematic* level, the *goal* level, or the *intention* level (cf. section 1.1; Kilner, 2011). These different levels of description bear a possible one-to-many mapping, which is problematic for the generation of predictions. For

instance, a cup can be picked up with different kinematics, depending on the goal of the action (to drink from the cup or to put it in a cupboard). At the same time, the same kinematics can be observed under different goals, for example, when a cup is picked up to be put away or to offer it to someone else. Hence, information derived from the kinematic or motor level alone is insufficient for successful action prediction (Kilner, 2011).

To overcome this problem, Kilner and colleagues (Kilner et al., 2007) developed a theory for action prediction that builds upon the predictive coding framework (cf. section 1.2.1). It is proposed that the hierarchical levels of action description can be mapped onto the hierarchy of cortical organization (Kilner et al., 2007; Kilner, 2011): higher-level action descriptions, like an action's goal, map onto higher cortical areas, whereas lower levels, like the kinematics, are mapped onto hierarchically lower cortical areas. An observed action is predicted on these multiple levels.

In order to successfully predict another person's actions, the most likely action goal needs to be inferred, for instance, drinking a glass of water (Kilner, 2011). Depending on the inferred goal, the most likely kinematics to accomplish this goal can be derived, e.g., reaching for and grasping a glass with the appropriate kinematics to achieve the goal (i.e., with a grip that allows for subsequent drinking instead of solely moving the glass). In line with the neural processing mechanisms proposed by predictive coding, it is assumed that a generative model based on the inferred goal is fed backwards to hierarchically lower areas and compared to the elicited neural activity (Kilner et al., 2007). Prediction errors between the generative model and the neural activity on lower levels are fed forward and lead to an adaptation of the predicted goal[2]. This process is repeated throughout all levels of the

[2] Kilner (2011) assumes that through this process even the intention of the actor could be derived, but he does not give a precise definition of intentions and how intentions can be clearly distinguished from action goals. Furthermore, it has been reported that inferring intentions, i.e.

cortical hierarchy until the prediction error is minimized and the correct action goal is derived.

According to Kilner, the AON does not achieve action prediction on its own, but more anterior regions of the prefrontal cortex are additionally involved in predicting an action's goal. Kilner supposes that possible goals that are associated with an object are passed from the posterior middle temporal gyrus (pMTG) to Brodmann areas (BA) 47 and 45. Here, the most likely goals are retrieved and selected and thereupon passed backwards to the premotor cortex, where the concrete action is predicted. This prediction is then fed back as generative model to posterior areas, such as inferior parietal and posterior temporal sites. Recent findings support this proposed processing cascade of fed-back predictions of actions from premotor to parietal and posterior temporal sites and fed-forward prediction errors (Gardner, Goulden, & Cross, 2015; Schippers & Keysers, 2011).

Although not addressed explicitly by Kilner (2011), the extension of the predictive coding framework to deriving goals and intentions of observed actions calls for its application to the prospection of future actions instead of mere prediction of causes of currently observed actions. Action goals are not fulfilled within one single motor act but require a number of separate action steps, e.g., switching on a kettle, putting a tea bag in a mug, pouring the hot water, and finally drinking the tea (Csibra & Gergely, 2007). It seems plausible to assume that the currently most likely goal is maintained on hierarchically higher-level cortical areas and aids on-line prediction of single action steps. Thus, the prediction spans a sequence of action steps. Within one action sequence, action steps are

mental states like believes or desires of a person, engages the theory-of-mind (ToM) network (de Lange et al., 2008), which is not part of Kilner's framework of predictive coding in actions. Thus, how inference of intentions and prediction of actions interact with each other needs further investigation.

probabilistically linked to each other (Baker, Tenenbaum, & Saxe, 2008; Baldwin & Baird, 2001). In line with the theory of predictive coding, it can be suggested that transition probabilities between action steps are learnt and updated with experience. Possibly, transitional probabilities could also be used to predict upcoming actions if no action goal or intention can serve as a basis for prediction.

### 1.2.3 Empirical evidence for predictive capacities

Although the theory of predictive coding is a comparatively recent one, behavioral signatures of human predictive capacities have been observed for a long time. A classic experiments to investigate prediction is the serial reaction time task (SRTT; Nissen & Bullemer, 1987). During an SRTT, locations on a screen are highlighted and participants are instructed to press as quickly as possible a button corresponding to the highlighted location. Unknown to the participants, the succession of button presses (or highlighted locations) follows certain regularities. After completing one block of the task, a decrease in reaction times can be observed (Nissen & Bullemer, 1987). In order to exclude that this decrease is solely due to a motor training effect the succession of the highlighted locations is switched to a random pattern in a later block, typically leading to prolonged reaction times (M. A. Stadler, 1992). In a last block the original pattern is re-established, resulting in quicker reaction times again. Hence, the SRTT is usually interpreted as providing proof of predictive processes: Participants seem to implicitly learn a pattern and use this pattern to prepare the respective motor response. This allows them to be quicker when the succession of highlighted positions accords to the learnt pattern.

Different variants of this classic paradigm have been developed, showing that perceptual regularities devoid of motor regularities (Koch & Hoffmann, 2000; Remillard, 2011) as well as pure observational learning of a sequence (Song, Howard, & Howard,

2008) can result in behavioral benefits. Furthermore, participants cannot only differentiate between ordered and random successions, but are even sensitive towards different degrees of transitional probabilities between succeeding locations (Hunt & Aslin, 2001). This capacity is not limited to simple transitional probabilities but also includes learning of more complex structures like 2nd-order conditional transition probabilities, where the probability of one particular location depends on the combination of the two trials before (Remillard, 2008).

Results from studies employing an SRTT endorse the notion of predictive processes during action selection and thus, the proposition of probabilistically weighted forward models (Wolpert & Flanagan, 2001). However, they do not undoubtedly prove predictive processes among non-motor cognitive functions. Additional support for human predictive capacities comes from paradigms investigating perceptual decision making, that is, how humans come to a categorical judgment (e.g., face vs. house, or left vs. right movement) of a perceptually more or less ambiguous stimulus (Summerfield & de Lange, 2014). Different experiments show that humans use spatial or temporal regularities to come to a decision, indicated through quicker and more accurate decisions for predicted compared to unpredicted stimuli (Bar, 2004; den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010; Kok, Jehee, & de Lange, 2012). Furthermore, humans' response patterns suggest that humans build expectations about a current stimulus based on the distribution of stimuli in the recent past which unconsciously affects the current perception (Chopin & Mamassian, 2012; Fischer & Whitney, 2014). These findings support the idea of human predictive capacities beyond the necessity to react towards an external event (Schubotz, 2007).

Over the past years, results from various imaging studies have provided further evidence for the predictive nature of human cognition and perception, and aimed to test

the predictions made within the framework of predictive coding. The theory claims the presence of two different kinds of signals, i.e. error signals and prediction signals (cf. section 1.2.1; Clark, 2013; Friston, 2005). Optimized predictions result in a minimization of surprise, i.e. prediction error. This allows for a metabolically more efficient processing of incoming information since only unpredicted aspects need to be signaled (Friston, 2005; Kok et al., 2012; Summerfield & Egner, 2009).

This central prediction has gained great attention over the past years. One early finding of fMRI research was the phenomenon of *repetition suppression*, that is, a reduced neural response to a repeated stimulus (Grill-Spector, Henson, & Martin, 2006). The neural mechanisms underlying repetition suppression remain unclear: the effect has been discussed to possibly reflect neural fatigue, sharpening of the neural response, or its facilitation (Grill-Spector et al., 2006). All these possible interpretations of the repetition suppression effect have in common that they focus on the effect of the repetition alone. Within predictive coding, repetition suppression is assumed to reflect not only the repetition of a stimulus but also an adaptation to the statistical structure of the environment (Summerfield & de Lange, 2014). Our environment is mostly stable; this means that the likelihood of one percept, for instance a chair, being still there when we look again is very high. Thus, expecting a stimulus to be repeated is a good initial prior (Summerfield & de Lange, 2014; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Consequently, the extent of repetition suppression should depend on the overall likelihood of a repetition. This hypothesis has been verified using faces (Larsson & Smith, 2012; Summerfield et al., 2008) and objects as stimuli (Mayrhauser, Bergmann, Crone, & Kronbichler, 2014). However, mixed evidence exists regarding the domain generality of this effect, and it has been suggested that it might depend on the implemented probability

of a repetition (Kovács, Kaiser, Kaliukhovich, Vidnyánszky, & Vogels, 2013), or the degree of expertise with a stimulus (Grotheer & Kovács, 2014).

Using magnetoencephalography (MEG), Todorovic and de Lange (2012) were able to distinguish two different factors contributing to the usually revealed attenuation of BOLD signal for repeated stimuli: 1) an effect of repetition, which occurs early in time and is independent of whether or not the repetition of the stimulus was expected, and 2) an effect of expectation, occurring later in time and depending on the expectation of the stimulus, irrespective of it being a predicted repetition or a predicted alternation. Along these lines, the authors argue that it should be distinguished between repetition suppression and *expectation suppression*. They assume that repetition suppression reflects physiological properties of the system, and expectation suppression is subject to experience and learning (Todorovic & de Lange, 2012). The finding of distinguishable effects of a stimulus' repetition and expectation has been extended to more complex sequences of predictable repetitions and alternations (Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015). This suggests that perceptual predictions can operate on longer timescales and reflect even more complex patterns.

While evidence for repetition or expectation suppression is substantial and supports the idea of prediction error units in the human brain, less direct evidence has been provided for prediction (or representation) units. Recent methodological advances allow for the decoding of pattern information from the BOLD signal (Norman, Polyn, Detre, & Haxby, 2006). Using this technique, it has been shown that a prediction error and a prediction signal can be concurrently decoded from stimulus-selective areas (de Gardelle, Waszczuk, Egner, & Summerfield, 2013). Valid prediction of a stimulus leads to an increase of information on the stimulus' identity in the activation pattern, although overall

activation is reduced (Kok et al., 2012). This suggests that sensory representations are sharpened in representation units (Kok et al., 2012).

A further central prediction of predictive coding is that hypotheses on sensations, i.e. generative models, are fed backwards from hierarchically higher cortical areas to lower areas (Friston, 2010). In support of this, it was shown that activation in stimulus-selective areas on hierarchically lower levels is modulated by higher cortical areas (Summerfield & Koechlin, 2008a; Summerfield et al., 2006).

In summary, numerous behavioral as well as functional studies provide evidence for human predictive capacities. Findings advocate that human perception is predictive and implemented across hierarchical levels of the brain. However, successful predictions require valid models of the environment. A possible account for the acquisition of these models will be presented next.

## 1.3 Learning what to predict

The theory of predictive coding explains in great detail how predictions are fed back through the cortical hierarchy and influence perception on the respective lower levels. Successful predictions require adequate models of the world. However, how humans acquire these models has received comparatively little attention within the framework of predictive coding. One of the most influential accounts explaining how knowledge about the structure of our environment is gained is *statistical learning*, which I will introduce in the following section.

### 1.3.1 Statistical learning

To successfully predict external events, accurate internal models of the world are necessary. One mechanism to acquire and update these models is through sensitivity

towards patterns of co-occurrence (i.e., contingencies) between events in space or across different timescales. The process of learning about these kinds of statistical regularities is termed *statistical learning*, which occurs unintentionally and usually without conscious awareness (Perruchet & Pacton, 2006). The terms *statistical learning* and *implicit learning* can be used interchangeably, as both describe the unintended learning of structure (Perruchet & Pacton, 2006).

Human ability for statistical learning has been shown in many different contexts. The probably most influential study was conducted by Saffran and colleagues (Saffran, Aslin, & Newport, 1996). In this study, infants were presented with a stream of syllables which were organized in fixed clusters of co-occurrence. After a phase of passive exposure to this stream, infants showed implicit knowledge of the cluster structure and were able to distinguish valid clusters from invalid ones. Thereby, the experiment provided an explanation for how language could be acquired during early development. In a similar vein, studies on *artificial grammar learning* show that humans are sensitive towards more complex rules that separate artificial grammatical from ungrammatical letter combinations (Perruchet & Pacton, 2006; Petersson, Folia, & Hagoort, 2012).

Further studies demonstrate that statistical learning is not limited to word-like stimuli, but also applies to learning of regularities between tones (Furl et al., 2011; Paraskevopoulos, Kuchenbuch, Herholz, & Pantev, 2012), abstract shapes (Turk-Browne, Scholl, Chun, & Johnson, 2009), and spatial configurations (Goujon, Didierjean, & Thorpe, 2015; Zhao, Cosman, Vatterott, Gupta, & Vecera, 2014).

A core brain region that seems to contribute to statistical learning is the middle temporal lobe, especially the hippocampus proper (Bornstein & Daw, 2012; Turk-Browne et al., 2009; Turk-Browne, Scholl, Johnson, & Chun, 2010). Activation in the hippocampus has been shown to increase with learning of statistical regularities (Turk-Browne et al.,

2009), and to signal successful prediction (Turk-Browne et al., 2010). Findings from a case study suggest that the hippocampus is mandatory for successful statistical learning (Schapiro, Gregory, Landau, McCloskey, & Turk-Browne, 2014). Together, these findings indicate that the hippocampus serves a core function in statistical learning.

Statistical learning could potentially also occur during action observation (Baldwin & Baird, 2001; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). This could explain how action knowledge, involving knowledge about objects, goals, or contexts, is acquired in the first place. A statistical learning account for action observation would fit with predictions made by motor control theory and the predictive coding framework. Both theories state that probability-weighted internal models underlie prediction of actions (Kilner, 2011; Wolpert & Flanagan, 2001).

It is still unclear what is exactly learnt during statistical learning. Most studies on statistical learning have focused on the learning of distinct chunks, i.e. pairs or triplets that co-occurred frequently. However, findings from studies using non-adjacent structures, that is, of type *AxxxB*, suggest that not only chunk information is acquired but that statistical computations are performed (Perruchet & Pacton, 2006). A recent study questions the importance of frequency information and conditional probabilities in statistical learning (Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013). The authors show that a common temporal context among succeeding images alone can cause the perception of chunks if transitions between images and their frequency are kept constant. This suggests that statistical learning can support learning of different aspects of a statistical structure.

As outlined so far, research on statistical learning provides strong evidence that human sensitivity to statistical structure is not limited to perception, but can also account for higher cognitive functions like language acquisition. In order to understand how statistical learning enables acquisition of models of the complex structures in our

environment, a formal description of a statistical structure is necessary. Recent attempts have been made to formalize the human ability to learn statistical structures, which will be presented in the next section.

### 1.3.2 Identifying levels of structure

Our understanding of how humans acquire precise models of their environment is still limited (Seriès & Seitz, 2013; Tenenbaum, Kemp, Griffiths, & Goodman, 2011). A formal description of *structure* is needed in order to identify which aspects of a statistical structure influence learning of the structure. A well-established approach to quantify aspects of a structure is provided by *information theory* (Shannon, 1948). Information theory allows distinguishing between the amount of information provided by one event, defined as *surprise*, and the overall degree of structure among events, quantified as *entropy*.

Surprise (I) relates directly to the probability *p*(x) of observing an event x, as it is defined as its negative logarithm:

$$I(x) = -\log\, p(x) \qquad \text{(Eq. 1)}$$

The less likely an event, the bigger its associated surprise. The value of information-theoretic surprise ranges between zero (when something was predicted with a probability of one) and infinity (if an observed event was not predicted at all, i.e. had a subjective probability of zero[3]). Equivalently, surprise reflects the amount of information transferred by an event. It could be shown that events that occur with a high surprise elicit a higher neural activation (den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; Strange, Duggins,

[3] Subjective probability takes into consideration that humans' estimated probabilities are always subject to incomplete experience and can thus not reflect the true state of the world, but only an approximation of it (Friston, 2010).

Penny, Dolan, & Friston, 2005). Observing surprising events leads to an adaptation of the internal model in order to minimize future surprises (O'Reilly et al., 2013).

Complementary to the concept of information, or surprise, is the one of uncertainty. Uncertainty can be described as a lack of knowledge or information about an upcoming event (Bland & Schaefer, 2012). Uncertainty drives learning and is thus a pre-requisite for statistical learning (Bland & Schaefer, 2012). In information theory, a similar concept to uncertainty has been coined as entropy (H), or the expected surprise across all possible outcomes:

$$H(\mathrm{X}) = -\sum_i p(x^i) \times \log p(x^i) \qquad \text{(Eq. 2)}$$

where $x^i$ is a particular event within a distribution (or random variable) X of possible events. While surprise refers to the single event alone, entropy depends on the whole distribution of probabilities for all possible events. Entropy increases with the number of possible events and is largest under equiprobability of events. This is consistent with the psychological concept of uncertainty (Hirsh, Mar, & Peterson, 2012). Entropy is zero when only one possible event is assumed (and accordingly, no surprise is expected).

The formulas of surprise and entropy can be extended to their conditional versions (Cover & Thomas, 1991). This adds further levels to the described structure and accords to the assumption that predictions can take a preceding event into account:

$$I(x_t|x_{t-1}) = -\log\, p(x_t|x_{t-1}) \qquad \text{(Eq. 3.1)}$$

$$H\left(X_t|x_{t-1}^j\right) = -\sum_i p\left(x_t^i|x_{t-1}^j\right) \times \log p(x_t^i|x_{t-1}^j) \qquad \text{(Eq. 3.2)}$$

$$H(X_t|X_{t-1}) = -\sum_j p\left(x_t^j\right) \times H\left(X_t|x_{t-1}^j\right) \qquad \text{(Eq. 3.3)}$$

where $x^i_t$ and $x^j_{t-1}$ are the events $x^i$ and $x^j$ observed at times *t* and *t-1* respectively, and $X_t$ and $X_{t-1}$ are the distributions of events at times *t* and *t-1* respectively. In this case, Eq. 3.1 corresponds to the surprise of seeing a certain event after seeing another event; Eq.

3.2 corresponds to the uncertainty (or entropy) of the next event given the previous event, also referred to as *forward entropy* (Bornstein & Daw); and Eq. 3.3 corresponds to the expected uncertainty of an event when the previous event is known, but not specified. This is referred to as *conditional entropy*. The lower the forward or the conditional entropy, the higher is the predictability of the next event given the preceding one.

The conditional entropy of a random variable is always equal to or lower than the entropy of that same variable (Cover & Thomas, 1991). Thus, to which extent conditional entropy reflects improved predictability of an upcoming event depends on the overall level of entropy among all possible events.

The concepts of entropy and surprise allow quantifying influences on learning of a statistical structure. The higher an event's surprise, the more it contributes to learning of the structure. Which levels of a structure are learnt depends on the respective degrees of entropy or conditional entropy.

Behavioral as well as functional findings corroborate the notion that humans are sensitive towards both the surprise as well as the entropy among a sequence of events (Bornstein & Daw, 2012; Nastase, Iacovella, & Hasson, 2014; Strange et al., 2005). Different studies report that hippocampal activation reflects the degree of entropy among a sequence of stimuli (Bornstein & Daw, 2012; Schiffer, Ahlheim, Wurm, & Schubotz, 2012; Strange et al., 2005). These findings add further to the hippocampus' functional profile: in light of the finding of hippocampal involvement in statistical learning, it can be suggested that the hippocampus is involved in the generation of predictions about possible events, which are more widespread under higher entropy (Schapiro & Turk-Browne, 2015).

The possibility to calculate the degree of forward entropy, that is, predictability, on multiple levels provides a quantitative explanation for the finding that humans can learn complex structural regularities (Dehaene et al., 2015; Perruchet & Pacton, 2006). Different

models of human cognition assume that humans initially attend to the simplest level of a statistical structure and only use higher levels of a structure if the lower structures do not allow for sufficiently accurate predictions (Gureckis & Love, 2010; Tenenbaum et al., 2011). In other words, more complex structural regularities are learnt if uncertainty, i.e. entropy, on lower levels is high.

This assumption can potentially explain how successful prediction of actions is achieved. As described in section 1.1.1, a wide array of action knowledge is available to inform predictions of an upcoming action, for example, an action's temporal or spatial context. Acquisition of this knowledge is highly complex due to the variability of the human action repertoire (Csibra & Gergely, 2007). In the following section, I will outline current evidence that action knowledge, like other kinds of abstract knowledge, can be acquired through sensitivity towards statistical structure of actions.

### 1.3.3 Statistical structure in actions

As outlined so far, numerous evidence points towards humans' sensitivity towards statistical structures. Concepts derived from information theory promote our understanding of how complex models of our environment can be acquired. However, to which extent this can also explain how humans gain such diverse action knowledge remains largely unaddressed. It has been proposed that actions follow statistical structures which can be learnt through mechanisms of statistical learning, and inform predictions of upcoming actions in the absence of action knowledge (Baldwin & Baird, 2001; Paulus et al., 2011; Zacks et al., 2007).

Like language, actions present themselves initially as a continuous stream of change without clear markers of a beginning or an end (Zacks et al., 2007). Still, we perceive and communicate actions in terms of chunks, or *events*, like "making coffee". This implies that

single action steps are grouped together through experience. Like in other domains, this chunking could be achieved through statistical learning (Baldwin, Andersson, Saffran, & Meyer, 2008; Buchsbaum, Griffiths, Plunkett, Gopnik, & Baldwin, 2014; Zacks et al., 2007). Statistical learning in actions requires integration of spatial information (e.g., which objects are involved in the action, how is an object grasped, or the current spatial context), as well as sequential information, like which actions have been executed before. This multidimensionality of actions could render statistical learning of actions more challenging, as the visual system is less specialized in tracking temporal compared to spatial regularities (Frost, Armstrong, Siegelman, & Christiansen, 2015). However, simultaneous learning across multiple dimensions can even be enhanced if the dimensions are correlated with each other (Turk-Browne, Isola, Scholl, & Treat, 2008), which is the case in actions.

In order to explain how the segmentation of a stream of observed activity into descriptive chunks can be achieved, Zacks and colleagues developed the *event segmentation theory* (Zacks et al., 2007). According to the event segmentation theory event schemas guide our perception of actions. Event schemas contain semantic memory representations that reflect previous encounters of similar actions and the actions' sequential structure. If a mismatch between an event schema and a currently observed action is registered, a boundary is perceived. This enables the perception of distinct events (Zacks et al., 2007). It can be hypothesized that the grouping of actions into events underlies our ability to disentangle action steps belonging to overlapping events, e.g., when a child observes her mother preparing breakfast and at the same time getting ready for work. Only if the child can disentangle the two different events, a prediction of the mother's future actions is possible.

Only few studies have investigated statistical learning in the context of action observation. Avrahami and Kareev (1994) were able to show that participants implicitly

learn a statistical structure underlying a succession of presented movie clips. This finding has been replicated and extended further (Baldwin et al., 2008; Buchsbaum et al., 2014). Moreover, it was shown that statistical regularities among gestures could guide attention, illustrating that knowledge about statistical regularities among actions is also used on-line while observing an action (Swallow & Zacks, 2008). However, it still remains unknown how statistical regularities among actions actually influence their neural processing and which regularities are used to predict an upcoming action in the absence of action knowledge.

# 2 Research Questions

This thesis tested for an influence of an action's statistical structure on its neural processing in the absence of any contextual or goal information. Besides this proof of principle, the aim was to identify which different aspects of a statistical structure affect an action's processing.

To that end, I conducted three fMRI experiments. In all experiments, participants were presented with videos of action steps. Successions of action steps followed respective pre-defined statistical structures. Participants gained implicit knowledge of these structures through passive viewing of the videos in separate training sessions. To construct sequences devoid of semantic expectations or knowledge, I used objects of the constructional toy *Baufix*®.

Within these three experiments, I addressed the following questions:

1) Do humans spontaneously detect statistical regularities underlying sequences of action steps and adapt to the resulting levels of probability and predictability of an action step?
2) Are humans furthermore sensitive towards higher-order information to improve predictability of an upcoming action step, and if so, do they exploit this information in a cost-benefit sensitive manner?
3) Do humans use a complex event structure that emerges from associations between action steps to predict upcoming actions?

In Experiment 1, I aimed at providing first evidence that statistical regularities among action steps indeed influence the processing of action steps within a continuous sequence of actions. More specifically, I created a statistical structure that allowed me to test whether an action step's transitional probability and predictability can be distinguished with regard to their effect on the action step's neural processing.

Consequently, I aimed to test how an action's predictability influences which possible sources of information about an action step are exploited. I hypothesized that low predictability of an upcoming action step should trigger search for further information, for instance provided by action steps from a more distant past. This led to the conduction of Experiment 2, where I investigated whether the use of information provided by the actions at *t-1* and *t-2* depends on the amount of information already provided by the action at *t-1* alone. I implemented a statistical structure where predictability of an action step based on the directly preceding action step (*t-1*) varied. The degree of the action's predictability could be improved by taking one further action step (*t-2*) additionally into account. This allowed me to test whether human observers spontaneously exploit both 1$^{st}$- and 2$^{nd}$-order statistical information to improve predictability of an upcoming action, and whether they do this in a cost-benefit optimized manner.

In Experiment 3, I tested whether humans improve their predictions of upcoming actions by using an event structure that emerges from associations between succeeding action steps. Alternatively, observers could only rely on information derived from preceding action steps. I designed a statistical structure that allowed grouping of action steps into distinct events based on the associations between them. Sequences of action steps belonging to one event were occasionally interrupted so that information on the current event could not be derived from preceding action steps alone.

# 3 Research Articles

## 3.1 Dissociating dynamic probability and predictability in observed actions – an fMRI study

frontiers in
HUMAN NEUROSCIENCE

ORIGINAL RESEARCH ARTICLE
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# Dissociating dynamic probability and predictability in observed actions—an fMRI study

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The present fMRI study investigated whether human observers spontaneously exploit the statistical structure underlying continuous action sequences. In particular, we tested whether two different statistical properties can be distinguished with regard to their neural correlates: an action step's predictability and its probability. To assess these properties we used measures from information theory. Predictability of action steps was operationalized by its inverse, conditional entropy, which combines the number of possible action steps with their respective probabilities. Probability of action steps was assessed using conditional surprisal, which increases with decreasing probability. Participants were trained in an action observation paradigm with video clips showing sequences of 9–33 s length with varying numbers of action steps that were statistically structured according to a Markov chain. Behavioral tests revealed that participants implicitly learned this statistical structure, showing that humans are sensitive toward these probabilistic regularities. Surprisal (lower probability) enhanced the BOLD signal in the anterior intraparietal sulcus. In contrast, high conditional entropy, i.e., low predictability, was correlated with higher activity in dorsomedial prefrontal cortex, orbitofrontal gyrus, and posterior intraparietal sulcus. Furthermore, we found a correlation between the anterior hippocampus' response to conditional entropy with the extent of learning, such that the more participants had learnt the structure, the greater the magnitude of hippocampus activation in response to conditional entropy. Findings show that two aspects of predictions can be dissociated: an action's predictability is reflected in a top-down modulation of attentional focus, evident in increased fronto-parietal activation. In contrast, an action's probability depends on the identity of the stimulus itself, resulting in bottom-up driven processing costs in the parietal cortex.

**Keywords: statistical learning, action observation, orbitofrontal cortex, dmPFC, fMRI, information theory**

## INTRODUCTION

When we observe another person's action, we are quite accurate at predicting what is going to happen next (Stadler et al., 2011; Zacks et al., 2011). But how do we know? Theoretically, we can be taught that an action A is typically followed by action B, as for instance when we learn how to bake a cake. However, we can also acquire knowledge about the structure of action sequences through statistical learning (Avrahami and Kareev, 1994; Baldwin et al., 2008). Statistical learning describes a mechanism of learning about associations between events through repeated experience of their co-occurrence or succession either in time or space (Turk-Browne et al., 2009; Fiser et al., 2010). Thereby, we learn about two statistical measures of actions that we can exploit to predict upcoming steps, given the current action step we observe: the number of possible action steps and their probabilities. The number and probability of the alternatively possible action steps at a particular moment (i.e., the degree of weighted branching at a node in the action sequence) determines the action's predictability, while in contrast to that, an action step's probability depends on the particular action step alone. For example, taking a banana is most often directly followed by peeling it, while taking an apple can be directly followed by a larger number of action steps, as, e.g., eating the apple, peeling, or cutting it. So after seeing someone grasping a banana, predictability of the next step is high, as only one action step is highly probable, while predictability of the next action step is lower after seeing someone taking an apple. To keep with the above example, despite the higher predictability after seeing someone grasping a banana, the probability of putting the banana in a lunchbox could be the same as putting an apple in a lunchbox. From a neuroscientific perspective, a differentiation between the two aspects is crucial: while an event's probability reflects how (un-)expected its occurrence was and hence, how much an observer needs to adapt his previously built expectations, predictability influences how precise an observer's expectations could be.

As this example illustrates, predictability and probability both quantify the statistical structure of actions, or more generally, events. While predictability (or its inverse, entropy, cf. Shannon,

1948) derives from the number of possible events and their respective probabilities, probability of an event (or its inverse, surprisal, cf. Tribus, 1961) refers to the event alone. Thus, predictability of an event can vary independently of its absolute probability. In actions, predictability is lowest at action boundaries (Zacks et al., 2011), depending on the weighted degree of branching at the node in the action sequence. The independence of predictability and probability is reflected by the observation that they differently affect encoding of stimulus streams (Strange et al., 2005; Harrison et al., 2006; Bornstein and Daw, 2012).

Various research has provided evidence that people are able to implicitly learn the statistical structure underlying incoming stimulus streams in both visual as well as auditory material (e.g., Hunt and Aslin, 2001; Saffran, 2001; Harrison et al., 2006; Swallow and Zacks, 2008; Bornstein and Daw, 2012; Paraskevopoulos et al., 2012; see Perruchet and Pacton, 2006 for a review). However, so far previous studies on statistical learning in actions have focused on learning of successions of separate action clips (Avrahami and Kareev, 1994; Baldwin et al., 2008; Swallow and Zacks, 2008), while evidence for statistical learning in dynamic action sequences is still lacking.

Building on this prior work, the goals of this study were two-fold. First, we aimed at establishing a role of statistical structure in the perception of continuous action sequences in general. Second, we wanted to address the question of neural correlates of predictability and probability of action steps at the current position of an action sequence. It has been shown that predictions of abstract visual events and actions rely in parts on identical brain sites, but engage also different ones (Schubotz and von Cramon, 2008). As most studies on predictability and probability in event streams made use of abstract visual stimuli, we aimed at extending knowledge on this further and examine, if the respective networks overlap or differ in their components.

To be able to dissociate predictability and probability of actions, we created action sequences according to a first-order Markov structure. That is, the predictability and probability of one certain action step depended on the preceding action step, i.e., they were conditional on their predecessor. We implemented two distinct measures for each quantity. Effects of action probability were measured as conditional surprisal, whereas action predictability was operationalized as conditional entropy (Shannon, 1948; Cover and Thomas, 1991). Conditional entropy combines the number of possible alternative action steps and their respective probabilities (for further details, see Materials and Methods and **Figure 1**).

We expected to find effects of the conditional surprisal of an action step in a lateral network often engaged by observing actions, including the premotor cortex, parietal sites, and the posterior temporal cortex (Jeannerod, 2001; Schubotz and von Cramon, 2004, 2008; Caspers et al., 2010). This network, also referred to as action-observation network, shows an increased response during the encounter of unexpected actions (Schiffer et al., 2013) and is furthermore also correlated with the surprisal of an abstract event (Strange et al., 2005; Bubic et al., 2011). Hence, we hypothesized activation in the action-observation network to show a higher activation for action steps with a higher surprisal.

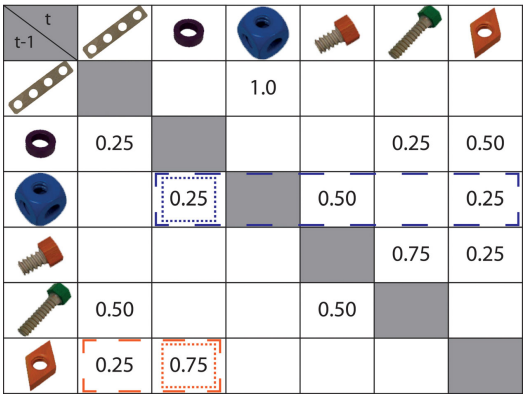


**FIGURE 1 | Markov chain ruling the presented action sequences.** Rows depict the first objects of a transition ($t$ - 1), e.g., the board (first row) was always ($p = 1.0$) followed by a cube (third column), whereas the cube (third row) could be followed by a washer ($p = 0.25$), a short screw ($p = 0.50$), or a screw nut ($p = 0.25$). Conditional surprisal of an action step depended on its probability given the preceding action step only. An example is highlighted in the figure: cells surrounded by dotted lines determine the surprisal assigned to the washer after a screw nut (orange) or a cube (blue). In contrast, an action step's conditional entropy depended on its own probability and the probability weights of alternative action steps. For instance, cells surrounded by dashed lines determine the conditional entropy assigned to the washer after the screw nut (orange) or cube (blue).

The degree of predictability of abstract stimuli has been found to draw on attentional and memory systems (Strange et al., 2005; Bornstein and Daw, 2012; Nastase et al., 2014), showing higher activations for less predictable stimuli. In line with this, Schubotz et al. (2012) found increased activation in left dorsolateral prefrontal cortex (dlPFC), parahippocampal gyrus, and posterior angular gyrus (AG) when observers noticed an action boundary in everyday actions (i.e., when predictability was low), and interpreted this as reflecting a shift of spatial attention that is guided by long-term action knowledge. However, this study did not address quantified predictability that results from the number and probability-balance of possible upcoming action steps. First evidence for a quantitative effect of the number of probable actions has been provided by Schiffer et al. (2012), who found an increase of activity in the hippocampal formation as the number of possible action steps increased and hence, predictability decreased. Based on these previous findings, we hypothesized activation in the hippocampal formation and the AG to correlate with predictability of observed action steps. Predictability was measured as conditional entropy, which is the inverse of predictability. Thus, we expected a positive correlation of the BOLD signal with conditional entropy. In psychological terms, conditional entropy can also be translated as conflict or uncertainty, as both rise, as more possible and probability-balanced alternatives are at hand (cf. Berlyne, 1957). Research on response conflict as well as on decisional uncertainty suggests a role of the posterior dorsomedial frontal cortex in adapting behavior to such situations (Ridderinkhof et al., 2004; Volz et al., 2005; Mushtaq

et al., 2011). We thus hypothesized activation in the dorsomedial prefrontal cortex (dmPFC) to be positively correlated with the conditional entropy of upcoming actions.

## MATERIALS AND METHODS

### PARTICIPANTS

Seventeen healthy right-handed participants volunteered in the fMRI study [mean age 25 (20–34) years, eight female, 14 students]. They were recruited from the volunteer database of the Max-Planck-Institute for Human Cognitive and Brain Science. No participant reported a psychiatric or neurological disorder. They gave written informed consent and received a financial reimbursement of 10€ per hour. The local Ethics Committee of the University of Leipzig approved the experimental standards. Two volunteers had to be excluded, one due to technical difficulties and one due to poor performance in the control task (score below two standard deviations from mean) and self-reported periods of sleep (results did not change qualitatively if participant was included in analysis). All following analyses of functional and behavioral data are thus based on data from 15 participants [eight female, mean age 25 (20–34) years].

### STIMULUS MATERIAL

The stimulus material consisted of videos showing sequences of action steps using objects of the constructional toy Baufix® (**Figure 1**). Overall, six different objects were used: a board, a cube, a long screw, a short screw, a nut, and a washer. An action step was defined as the grasping and mounting of one object. Each object was always manipulated in the same way: the cube was screwed on the scaffold, the long screw was put through a hole of a board, washer and boards were placed on long screws, screw-nuts were attached to screws, and short screws were screwed into cubes. Action steps were performed in a naturalistic manner and hence differed in their length and speed of movement.

Videos showed sequences comprised of varying combinations and numbers of these six action steps. The transitions between action steps followed a Markov chain (see **Figure 1**) and were the same for all subjects. Transition probabilities between action steps were pre-defined and ranged from $p = 0.25$ to $p = 1$. Except mounting of the cube, which was always preceded by the same action step, each action step was preceded by one out of two to three different action steps and depending on the preceding action step, one, two or three different action steps were concurrently possible, causing different values of conditional entropy and surprisal (see section "Contrast Specification"). Importantly, this statistical structure enabled us to disentangle values of conditional entropy and surprisal from identity of action steps and involved objects, as well as the characteristics of the action steps as speed of movement and length of manipulation. Repetitions of action steps within a sequence were possible but were not correlated significantly with our measures of interest (correlation with conditional entropy $r = 0.03$, correlation with conditional surprisal $r = -0.12$). Direct repetitions of action steps did not occur. To implement the Markov chain, 74 construction sequences were compiled. Action sequences differed in the number of action steps they comprised, ranging from three to seven ($M = 4.89$, $SD = 1.28$), and their overall presentation duration ($M = 20.12$ s, $SD = 6.04$). Note that constructions did not aim to reach a specific, pre-defined overarching goal, as for instance building a vehicle.

Overall, each action step was presented about 60 times (58–63, $M = 60.33$), so that all action steps had a comparable base rate. We moreover balanced how often an action step emerged as the first or the last step of a construction sequence (first: 10–15, $M = 12.5$; last: 10–15, $M = 12.33$).

To have ample degrees of freedom for the construction process, the first action step was always performed on a prepared "starting" scaffold consisting of various different mounted objects (as can be seen in **Figure 2**). Sequences started at the moment the actor lifted the scaffold and ended when the scaffold was placed on the table again. In sum, five different starting scaffolds were employed. Each of the 74 action sequences was filmed once with each of these five scaffolds (resulting in 370 videos altogether), so that participants never saw the exact same shot of one action sequence twice. Hence, expectations within action sequences could only be based on the employed transition probabilities between action steps.

Videos were filmed from the third person perspective with no zooms or camera motions. The focus was on the center of the table and offered a good view of the actor's hands, but not the head, and numerous different objects in the foreground (see **Figure 2**). The software iMovie ′09 (Apple, Inc., Cupertino, CA) was used for video processing.

Randomization of order of the sequences during the experiment was constrained by allowing maximal two repetitions of the used scaffold, the sequence length as well as the first and last element of the sequence. Additionally, the cases of the former sequence being a subsequence of the latter and vice versa were excluded.

### EXPERIMENTAL PROCEDURES

The experiment took place on three successive days. The first two sessions served as training to provide participants with implicit knowledge of the underlying statistical structure of the action sequences. On the third day, participants first underwent the fMRI experiment. Afterwards, they took part in two post-tests, which tested their implicit knowledge of the action syntax. The experiment was programmed and run on Presentation 12.0 (Neurobehavioral Systems, San Francisco, CA, USA).

### TRAINING SESSIONS (DAY 1 AND 2)

During each of the two 35-min training sessions, participants were exposed once to each of the 74 sequences. Participants were exposed to a different randomization of movies in each training session.

Participants were instructed to watch the videos carefully and to answer the occasional questions concerning the previous video. Questions appeared after 36 of the 74 video clips (48%). It is important to note that participants did not receive explicit learning instructions at any point of the training (or the subsequent fMRI session), nor were they told that there was a certain systematic concerning the statistical structure of the action sequences. No cover story was provided.

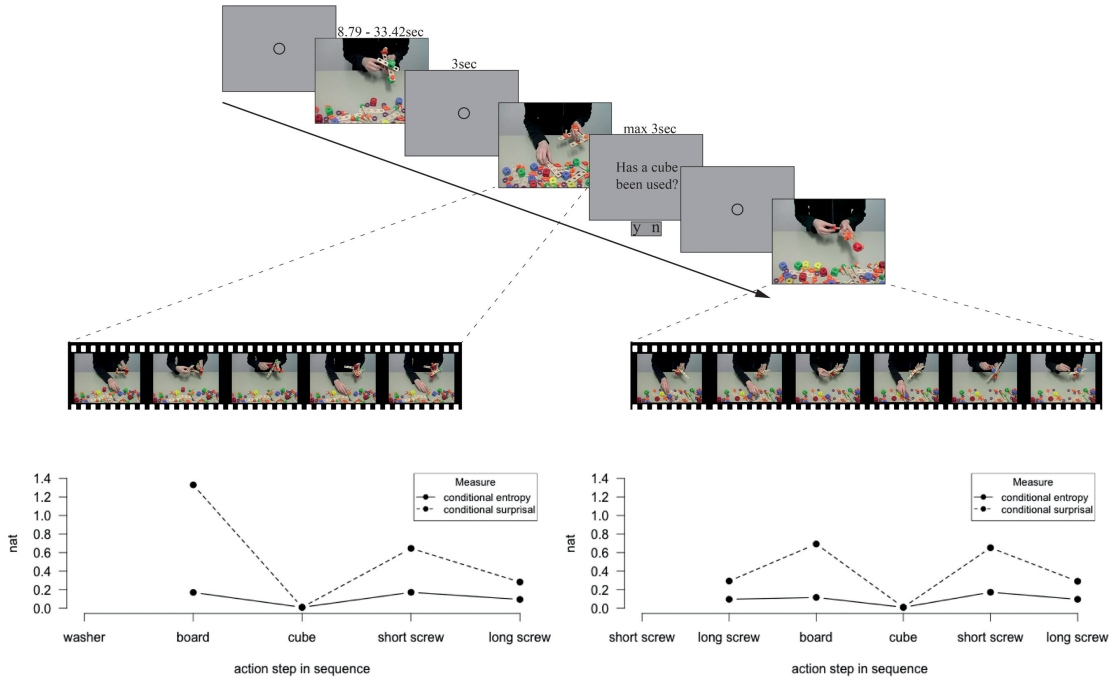


**FIGURE 2 | Experimental course and exemplary distribution of conditional entropy and conditional surprisal during an action sequence.** A fixation circle announced each video and 48% of the videos were followed by a two alternative forced choice question. Feedback on correctness of responses was only given during the training sessions. Within each action sequence, values of conditional entropy and conditional surprisal were ascribed to the action steps, depending on the preceding action step.

Before starting the training, participants were familiarized with the six different objects as well as with the possible questions (e.g., "Has a long screw been used?"). During training, participants had to press the right mouse button (i.e., middle finger of the right hand) corresponding to the answer "no" and the left mouse button (i.e., right index finger) corresponding to "yes." Half of the questions required an affirmative answer.

The videos were displayed in front of a gray background in the middle of a computer screen (subtending approximately 12.5*10° of visual angle). A fixation circle announced videos for 3 s (or variable length after question trials; see **Figure 2** for an illustration of the trial course). Questions were presented for 3 s or until the first response; after question trials, the duration of the fixation circle was adapted to compensate for different reaction times (with keeping a minimum duration of 2 s). Questions were followed by a feedback of 2 s indicating correct ("+"), incorrect ("−"), or delayed ("/") responses.

#### FUNCTIONAL MRI SESSION (DAY 3)

The task in the fMRI session was identical to the training sessions, except that no feedback was provided. Participants were informed about this difference beforehand.

In addition to the experimental block, we ran four functional localizers adapted from Wurm and Schubotz (2012) after the main experiment so as to identify brain regions related to the processing of Baufix® objects, other tools, motion, and human body (see Supplemental Material for Analysis and Results).

Following the functional scanning, two post-tests assessed participants' implicit knowledge of the action syntax. During the first post-test, a paper–pencil test, six video clips were presented in randomized order. These clips ended after one object had been used and the actor reached for a second one. The participants' task was to mark those objects out of the possible six that they expected to be used next and to indicate their respective probability. To this end, they had to assign overall eight crosses among the six items. For instance, if participants saw a clip in which the long screw had been used and they expected the board and the short screw afterwards with equal probability, they assigned four crosses to each of them. The number of eight crosses was chosen to allow participants to select up to all six possible objects and to weight them accurately (each cross corresponded to $p = 0.125$). In the second post-test, participants were presented each possible succession of two of the six objects and were asked to enter a value between 0 and 100% representing how likely they considered each succession with regard

to the previously seen videos. Responses were given via keyboard, and participants could revise their answer before finally submitting it.

After completing the post-tests, participants were interviewed to further assess if they have consciously noticed the statistical structure of the presented action sequences and if so, to which degree they were able to specify the structure. To this end, they were asked verbally if they have noticed any associations between the action steps and if so, if they could define them. Furthermore, they were asked if the actions were predictable for them.

#### BEHAVIORAL DATA ANALYSIS

The statistical analysis of the two post-tests was performed with SPSS Statistics version 20.0 (SPSS Inc. Chicago, Illinois, USA). An α-level of 0.05 was defined as statistical threshold.

First, we aggregated separately for each post-test for each participant the estimated probabilities of the transitions, depending on the underlying level of implemented probabilities (0, 0.25, 0.50, 0.75, or 1.0), e.g., we calculated the average estimated probability for all transitions with the same true probability. Those aggregated probability estimates were entered in a separate repeated measures analysis of variance (RM-ANOVA) with the factor PROBABILITY (0, 0.25, 0.50, 0.75, 1.0) for each post-test. When the assumption of sphericity was violated, a Greenhouse-Geisser correction was used to adjust the degrees of freedom.

#### FUNCTIONAL DATA ANALYSIS

##### *Contrast specifications*

Predictability of action steps was manipulated by the number of possible next action steps and their respective probabilities. Conditional entropy (H) provides a measure that takes both aspects into account and is higher, the lower the predictability is. In contrast, probability of the factually occurring action step was modeled as conditional surprise (I, surprisal hereafter, cf. Tribus, 1961), which is the negative logarithm of an action step's probability. The applied modeling of conditional entropy and conditional surprisal was in close proximity to the approach taken by previous studies (Strange et al., 2005; Harrison et al., 2006; Bornstein and Daw, 2012; Schiffer et al., 2012).

Conditional entropy and surprisal are only partially statistically independent, because the probability of a single action step decreases as the number of possible action steps increases. The advantage of modeling correlated parameters simultaneously in one general linear model (GLM) is that any variance that is explained by both parameters will not be erroneously assigned to exclusively one of them. At the same time, this approach has the disadvantage that it does not show areas that are truly modulated by both conditional entropy and surprisal. That is, commonalities will be underestimated (false negatives). To avoid this latter fallacy, we additionally tested for effects of conditional entropy and conditional surprisal by employing a separate design for each and provide results in the Supplementary Materials. Both approaches resulted in similar results, but showed also some differences.

##### *Calculating probabilities: Bayesian modeling approach*

We modeled the neural responses according to an ideal observer model, which tracks the number of occurrences of events and calculates probabilities based on all occurrences (cf. Strange et al., 2005; Harrison et al., 2006; Bornstein and Daw, 2012; Schiffer et al., 2012). Hence, the probability $p$ of a single item $x_t$ was calculated as the number of occurrences $n$ of item $x_t$ divided by the sum of all items $x_i$ that have appeared so far (see Equation 1). The addition of the value 1 shapes a Dirichlet function.

$$p\,(x_t) = \frac{n(x_t) + 1}{\sum_i x_i + 1}$$

Equation 1. Calculation of Bayesian probabilities.

The ideal observer model included the training sessions, so transition probabilities were already taken as established at the beginning of the fMRI session. Since all action steps had a similar base rate, we did not calculate the surprisal of the occurrence of an action step *per se*, i.e., $p(x_t)$. Instead, we calculated the conditional surprisal ascribed to a transition, i.e., the occurrence of an action step, given that a particular action step had happened before, $p(x_t|x_{t-1})$ (Equation 2). Values for surprisal ranged from 0.01 to 1.38 ($M = 0.63$, $SD = 0.49$).

$$I\,(x_t|x_{t-1}) = -log\; p\,(x_t|x_{t-1})$$

Equation 2. Calculation of conditional surprisal.

In analogy, we did not calculate the entropy ascribed to the underlying Markov chain of the action sequences, but focused on the specific conditional entropy (Cover and Thomas, 1991). Conditional entropy refers to the entropy ascribed to an upcoming event when the prior event is taken into account. It describes the (on average) expected surprise. It is calculated as mean surprise of all possible events $x_t$ given that $x_{t-1}$ had occurred, standardized on the probability of the prior event $p(x_{t-1})$ (Equation 3). Values ranged from 0.01 to 0.72 ($M = 0.11$, $SD = 0.05$). Correlation of both parameters was $r = 0.67$.

$$H\,(x_t|x_{t-1}) = -p\,(x_{t-1}) \sum_i p\left(x_t^i|x_{t-1}\right) * log\; p\left(x_t^i|x_{t-1}\right)$$

Equation 3. Calculation of conditional entropy.

#### fMRI DATA ACQUISITION AND ANALYSIS

A 3 T Siemens Magnetom Trio (Siemens, Erlangen, Germany) system equipped with a standard birdcage headcoil was used in the functional imaging session. Participants lay supine in the scanner with their right hand on a four-button response-box and their index and middle finger placed on the two appropriate response buttons. Response contingencies were the same as in the training sessions. Form-fitting cushions were used to prevent participants from head or arm movements and they were provided with earplugs to attenuate scanner noise. The experiment was presented via a mirror that was built into the headcoil and adjusted individually to provide a good view of the entire screen.

Prior to functional imaging, 28 slices of anatomical T1-weighted MDEFT images (4 mm thickness, 0.6 mm spacing) and a fieldmap scan, consisting of a gradient-echo readout with 24 echoes and an inter-echo time of 0.95 ms, were acquired. During functional imaging, 28 axial slices (126.8 mm field of view, 4 mm

thickness, 0.6 mm spacing; in-plane resolution of 3 × 3 mm) parallel to the bi-commissural line (AC-PC) were collected using a single-shot gradient echo-planar (EPI) sequence (2000 ms repetition time; echo time 30 ms, flip angle 90°, serial recording), sensitive to BOLD contrast.

To improve the localization of activation foci, high-resolution 3D T1-weighted whole brain MDEFT sequences (175 sagittal slices, 1 mm thickness) were recorded for each participant in a separate session.

Functional data were processed using the LIPSIA software package, version 2.1 (Lohmann et al., 2001). First, a distortion correction using the field map scan was performed. To correct for temporal offsets between the slices acquired in one scan, a cubic-spline interpolation was used. Thereafter the data were motion-corrected with the $50^{th}$ time-step as reference and six degrees of freedom (three rotational, three translational). A high-pass filter of 1/70 or 1/55 Hz (different between participants) was applied to remove low-frequency signal changes and baseline drifts. Highpass filter width was determined by an optimization algorithm implemented in the LIPSIA package.

Functional data slices were aligned with a 3D stereotactic coordinate system. To that end, in a first step the matching parameters (six degrees of freedom, three rotational, three translational) of the T1-weighted 2D-MDEFT data onto the individual 3D-MDEFT reference set were calculated. The thereby gained transformation matrix for a rigid spatial registration was normalized to a standardized Talairach brain size ($x = 135$, $y = 175$, $z = 120$ mm; Talairach and Tournoux, 1988) by linear scaling. Thereafter the normalized transformation matrices were applied to the functional slices, in order to transform them using trilinear interpolation and align them with the 3D-reference set in the stereotactic coordinate system. After the described processing, the spatial resolution of the functional data was 3 * 3 * 3 mm ($27\ mm^3$). A spatial Gaussian filter of 5.65 mm full width at half maximum (FWHM) and a standard deviation of 0.8 mm was applied to the data.

#### *Design specifications*

We modeled the parametric contrasts of conditional surprisal and conditional entropy time-locked to the beginning of a new action step. Onsets were defined as the starting of the hand movement to the next object. If two events were separated by less than 2 s (i.e., less than one TR), only the first one was included in the GLM, while the second was ignored and treated as part of the implicit baseline. To control for variance due to action observation in general, we also modeled the video clips as epochs (mixed design). The parametric contrasts of conditional entropy and conditional surprisal contained 219 events with a mean difference between events of 7.93 s (5.01 s *SD*), which were selected from 74 video epochs.

The statistical evaluation was based on the least-square estimation using the GLM for serially auto-correlated observations and a temporal Gaussian filter with a FWHM of 4 s was applied to deal with auto-correlation (Friston et al., 1995; Worsley and Friston, 1995).

To calculate the parametric effects of conditional surprisal and conditional entropy, the design matrix was generated with a delta function and its first derivative, convolved with the hemodynamic response function (gamma function) (Glover, 1999). The BOLD signal was analyzed time-locked to the specific events. The design matrix included six regressors: one for the main effect of action onsets with an amplitude of one, one for the parametric effect of conditional entropy, one for conditional surprisal, with an amplitude according to the respective measure, and two each with an amplitude of one for question trials and video epochs. The duration of action steps was included as a regressor of no interest. Besides the video epochs and the question trials, all events were modeled with a duration of 1 s. Question trials were modeled with a duration of 3 s and video epochs were modeled with the duration of the respective video clip. The model equation consisted of the observed data, the design matrix, and the error-term.

For each participant, contrast images were generated, which consisted of beta-value estimates of the raw-score differences between experimental conditions. Subsequently, the individual contrast images were entered into a second-level random effects analysis. Here, one-sample *t*-tests across the contrast images of the 15 participants were performed to test the observed differences for significant deviations from zero. The *t*-values were transformed afterwards into z-scores.

We corrected for multiple comparisons by applying a two-step correction approach. An initial z-threshold of 2.33 ($p < 0.01$, one-tailed) was defined in the first step. All voxels showing a positive activation above this threshold entered the second step of the correction. Here, a Monte Carlo simulation was used to define thresholds for cluster-size and cluster-value at a significance level of $p < 0.05$ (one-tailed). The combination of cluster size and cluster value decreases the risk of neglecting true activations in small structures. Thus, all reported activations were significant at $p < 0.05$, corrected for multiple comparisons at the cluster level.

#### *ROI analysis*

To test for activations in the anterior hippocampus, we performed an additional region of interest (ROI) analysis for conditional entropy. The ROI in the left anterior hippocampus was defined by averaging coordinates of peak activation reported in previous studies on predictability of sequences of visual stimuli (Strange et al., 2005; Harrison et al., 2006; Bornstein and Daw, 2012); coordinates for the ROI in the right anterior hippocampus were derived from the study by Strange and colleagues. Center of the ROI in the left anterior hippocampus was at $x = -25$, $y = -16$, $z = -18$, center of the ROI in the right anterior hippocampus was at $x = 31$, $y = -17$, $z = -19$. Both ROIs had a sphere of six adjacent voxels. One-sample *t*-tests were calculated over beta-values per participant and ROI to test for significant deviations from zero.

Additionally, we tested *post-hoc* for correlation between beta-values derived from the parametric contrast of conditional entropy and the degree of familiarity with the statistical structure as assessed by the two post-tests. We quantified the degree of familiarity with the statistical structure separately for both post-tests as difference between the maximal probability judgment (100 for the computer and 8 for the paper–pencil post-test) and the average absolute deviation of the probability judgments ($\hat{p}$)

from the implemented probabilities ($p$) (Equation 4).

$$Familiarity = p_{max} - \frac{1}{n}\sum_{n}|\hat{p}_n - p_n|$$

Equation 4. Calculation of the degree of familiarity with the statistical structure. Parameter $\hat{p}$ describes participants' probability judgments, parameter $p$ the implemented probabilities of the different transitions ($n$) and $p_{max}$ the maximal judgment in the respective test (with a value of 100 for the computer and 8 for the paper–pencil post-test).

## RESULTS

### BEHAVIORAL RESULTS

During the fMRI, participants answered on average 34.47 out of 36 questions correctly ($SD = 1.77$). One participant answered only 30 questions correctly ($z$-value $< -2$) and was excluded from all further analyses.

In order to assess whether participants learned the statistical structure of the actions, two post-tests were conducted.

Regarding the paper–pencil post-test, two participants had to be excluded from analyses, as they were erroneously presented only five instead of six objects. For the remaining participants, the RM-ANOVA on the estimated probabilities was significant [$F_{(1.69,\ 20.26)} = 19.52$, $p < 0.001$, $\eta_p^2 = 0.62$]. Planned comparisons between the different levels yielded significant differences between the levels of 1.0 and 0.75 [$t_{(12)} = 2.50$, $p = 0.014$, one-tailed] and the levels of 0.50 and 0.25 [$t_{(12)} = 6.56$, $p < 0.001$, one-tailed; see **Table 1** for means and standard deviations].

The RM-ANOVA on the estimated probabilities of the computer post-test was also significant [$F_{(2.43,\ 34.05)} = 26.90$, $p < 0.001$, $\eta_p^2 = 0.66$]. Two out of four planned comparisons between the different levels of probability reached significance: 1.0 vs. 0.75 [$t_{(14)} = 3.36$, $p = 0.003$, one-tailed] and 0.50 vs. 0.25 [$t_{(14)} = 6.1$, $p < 0.001$, one-tailed; see **Table 1** for means and standard deviations of the five levels, **Figure 3** for a graphical display].

Together, both post-tests consistently showed that participants rated transitions with higher probabilities as more likely, while they were not able to exactly distinguish between each probability level.

**Table 1 | Descriptive results of the two post-tests, separately for the five levels of implemented probabilities.**

| Implemented probability | Distributed crosses in paper–pencil post-test: Mean (*SD*) | Estimated percentages in computer post-test: Mean (*SD*) |
|---|---|---|
| 0 | 0.95 (0.22) | 22.03 (7.76) |
| 0.25 | 0.86 (0.46) | 22.77 (9.35) |
| 0.50 | 2.79 (0.70) | 44.12 (11.10) |
| 0.75 | 2.65 (1.20) | 44.17 (17.81) |
| 1.0 | 4.54 (2.33) | 59.80 (23.74) |

### IMAGING RESULTS

#### *Parametric effects of conditional surprisal*

Assessing parametric effects of conditional surprisal revealed a positive correlation in the bilateral anterior intraparietal sulcus (see **Figure 4A** and Figure S3 for additional sagittal views; a comprehensive list of activations and Talairach coordinates are provided in **Table 2**, see Table S5 for MNI coordinates).

#### *Parametric effects of conditional entropy*

We found a positive correlation of conditional entropy with BOLD response in the right lateral and medial orbitofrontal cortex (lOFC and mOFC, hereafter), dmPFC, bilateral inferior frontal gyrus (IFG), bilateral anterior dorsal insulae, and right posterior intraparietal sulcus (pIPS) (see **Figure 4B**); a comprehensive list of activations and Talairach coordinates are provided in **Table 2**, see Table S5 for MNI coordinates.

#### *ROI analysis*

No significant hippocampal activation was revealed by the ROI analysis (all $p > 0.4$; see **Table 3** for descriptive statistics of beta weights). The *post-hoc* correlation analysis revealed a significant positive correlation between familiarity with the statistical structure, measured as average deviation from the implemented probabilities (see Equation 4), in both ROIs when familiarity was assessed with the computer post-test (all $p < 0.05$), but not when it was assessed with the paper–pencil post-test (all $p > 0.33$, see **Table 4**). This correlation indicates that activation in the hippocampal ROIs was the stronger positively correlated with conditional entropy, the better participants had learnt the statistical structure of the action sequences.

## DISCUSSION

From a stochastic point of view, the course of an action can be conceived of as a run through a decision tree: one step follows another with a certain probability while more or less alternative

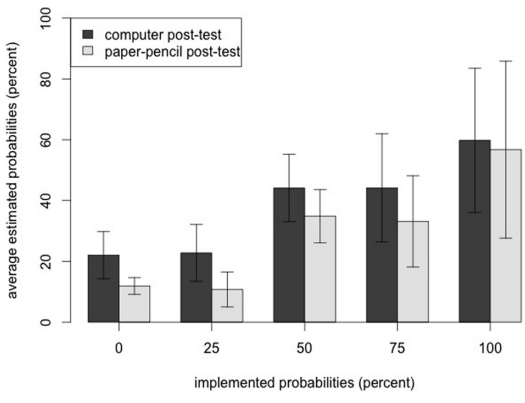


**FIGURE 3 | Results of the two post-tests.** As one cross in the paper–pencil post-test corresponded to 12.5% in the computer post-test, results of the paper–pencil post-test were multiplied with the factor 12.5, to make participants' probability judgments in the two post-tests more comparable. Error bars display ± 1 *SD*.

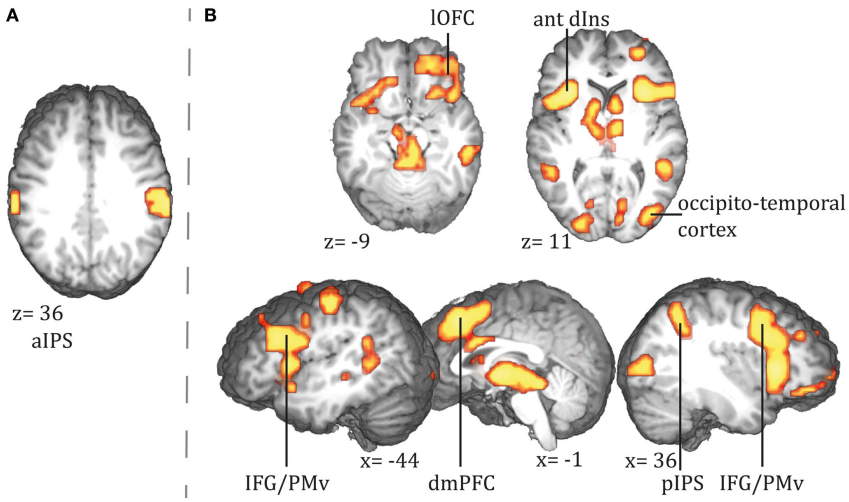


**FIGURE 4 | Areas showing a positive correlation with (A) conditional surprisal and (B) conditional entropy.** ant dIns, anterior dorsal insula; dmPFC, dorsomedial prefrontal cortex; IFG, inferior frontal gyrus; lOFC, lateral orbitofrontal cortex; pIPS, posterior intraparietal sulcus; PMv, ventral premotor cortex; aIPS, anterior parietal sulcus.

action steps are possible. In the present fMRI study we assumed that an action's statistical structure is reflected in the brain activity of the action observer. In particular, we aimed at deciphering two distinct aspects of the statistical structure that may influence processing of action steps. First, the load of this processing varies as a function of the action step's absolute probability at the point of the sequence, and hence unexpectedness or conditional surprisal. Second, the observed action step is more or less predictable, depending on the degree of branching of the decision tree at the considered action boundary and the probability weights of these different branches. This latter characteristic can be quantified as conditional entropy, which is higher, the less predictable an upcoming action step is.

We employed an ideal Bayesian observer model and analyzed the BOLD response for (1) the conditional surprisal and (2) the conditional entropy at beginnings of action steps. We found activation in the aIPS to positively correlate with an action step's conditional surprisal. For conditional entropy, we expected a positive correlation with activity of the AG, the hippocampal formation, and the dmPFC. We found activation in the right dmPFC and in the pIPS, close to the AG. No effect in the hippocampal formation was found. Instead, activity also increased with conditional entropy in the right lOFC and the bilateral anterior dorsal insulae. Findings will be discussed in detail below.

#### BEHAVIORAL FINDINGS: PARTICIPANTS' AWARENESS OF PROBABILISTIC ACTION STRUCTURE

A post-fMRI survey revealed that participants had little awareness of the probabilistic structure of the actions. However, they were able to report those pairwise associations between the action steps with highest transition probabilities (board–cube, short screw–long screw, washer–screw nut). No participant reported having noticed the different probabilities or degrees of predictability. Still, the two post-tests showed that participants implicitly learned the transition probabilities, as more likely transitions were judged to occur with a higher probability than less likely transitions. These judgments delivered in a computer test were moreover confirmed in a subsequent paper–pencil test, in which more likely transitions were selected more often than less likely transitions. Behavioral data indicate that the probabilistic structure of observed action is acquired and retrieved during action observation, even if not explicitly attended or consciously perceived.

The present findings add up to studies on statistical learning in actions (Avrahami and Kareev, 1994; Baldwin et al., 2008). Previous findings suggested that human observers can distinguish between random and deterministic transitions between distinct video clips showing object manipulations or movie excerpts. Our results indicate that human observers are also sensitive to statistical structure within continuous action sequences; furthermore, they are able to distinguish between different degrees of transition probabilities between action steps. This means that human observers can detect meaningful segments within uniform streams of actions based on statistical information. Critically, we did not distinguish between transitions between objects and transitions between object manipulations. Further studies should test for potential differences in effects of transition probabilities.

#### CONDITIONAL SURPRISAL: PROBABILITY-DEPENDENT ENGAGEMENT OF THE ANTERIOR INTRAPARIETAL SULCUS

Expectations can serve as a filter for sensory input, inasmuch as everything that accords to the expectations is largely uninformative. By filtering on an early stimulus processing level, unexpected and hence informative sensory signals get more accentuated (Wolpert and Flanagan, 2001; Friston and Kiebel,

2009; Summerfield and Egner, 2009). This results in greater neural activity for unexpected events compared to expected events in stimulus- and task-relevant brain areas. As observing actions is known to engage the lateral network of premotor cortex, parietal sites, and posterior temporal cortex (Jeannerod, 2001; Schubotz and von Cramon, 2004; Caspers et al., 2010), we expected effects of conditional surprisal of an action step to be found here. Importantly, all action steps in the present study had an equal base rate, so that effects were not due to unexpectedness of the action step *per se*. Rather, we tested if expectations can be built based on transition probabilities between action steps. If so, action steps with a higher conditional surprisal should accordingly elicit a higher BOLD response in the action-observation network, as they were comparatively unexpected at that very point in time, and the conveyed information would not have been selectively filtered in advance (Schiffer et al., 2013).

We found enhanced BOLD response for unexpected action steps in the aIPS. The anterior portion of the IPS has been supposed to be the homolog to area AIP in macaques, which is sensitive to size, shape, and orientation of objects (Grefkes and Fink, 2005). In humans, it is proposed to deal with processing of tactile and visual object properties (Grefkes and Fink, 2005) and has been related to the online control of grasping and coding for goals in actions (Hamilton and Grafton, 2006; Tunik et al., 2007). Furthermore, aIPS together with temporo-occipital sites and the premotor cortex forms a network which is most commonly activated during action observation (Caspers et al., 2010). In accordance with current accounts of predictive coding during action observation, processing in this network is hierarchical (Kilner et al., 2007), meaning that information about object properties is fed forward from temporo-occipital sites to aIPS and from there to the premotor cortex. While activation in PMv and temporo-occipital cortex was modulated by conditional entropy of action steps, activation in aIPS covaried with unexpectedness of action steps. We suggest that increased activation in the aIPS for unexpected action steps reflect a revision of the previously built sensorimotor forward model of the expected manipulation of the object.

Given that we found the expected covariation with conditional surprisal of an observed object manipulation in the aIPS, it remains unclear why there was no such effect in earlier visual areas. It is possible that the statistical structure was not assigned to the relation between successively manipulated objects, but rather between successively performed action steps, i.e., a compound of object and its manipulation. A revision of the built forward model should draw to a larger extend on aIPS than temporo-occipital areas. In line with this, Schubotz and von Cramon (2008) found activation of aIPS in a switching paradigm particularly then when both the goal of an action as well as the involved object remained the same, while it did not reach significance anymore when one of the two changed. The aIPS was the only component of the action observation network that showed this activation pattern,

**Table 2 | Talairach coordinates and maximal *z*-scores of significantly activated voxels for the parametric contrasts of conditional surprisal and conditional entropy (combined GLM approach).**

| Localization | Talairach coordinates | | | *z*-values, local maxima |
|---|---|---|---|---|
| | *x* | *y* | *z* | |
| **CONDITIONAL SURPRISAL** | | | | |
| Anterior intraparietal sulcus/postcentral gyrus | 55 | −24 | 39 | 4.28 |
| | −59 | −27 | 36 | 3.08 |
| **CONDITIONAL ENTROPY** | | | | |
| Dorsomedial prefrontal cortex | 1 | 24 | 45 | 4.43 |
| Postcentral gyrus | −47 | −18 | 54 | 3.96 |
| Anterior dorsal insula | 31 | 18 | 6 | 5.15 |
| | −29 | 21 | 9 | 5.28 |
| Posterior intraparietal sulcus | 40 | −48 | 33 | 3.51 |
| Inferior frontal sulcus/ventral premotor cortex | −44 | 21 | 27 | 4.24 |
| Anterior cingulate cortex | −5 | 15 | 24 | 3.65 |
| Middle frontal gyrus | 22 | 48 | 21 | 3.54 |
| Posterior superior temporal sulcus | 40 | −48 | 33 | 3.51 |
| | −47 | −45 | 27 | 2.86 |
| Inferior colliculi | 1 | −39 | −6 | 4.21 |
| Lateral temporo-occipital cortex | 34 | −81 | 9 | 3.29 |
| Dorsal medial thalamus | −11 | 6 | 6 | 3.14 |
| Cuneus | −23 | −90 | 3 | 3.67 |
| Medial orbitofrontal cortex | 16 | 39 | −9 | 3.55 |
| Lateral orbitofrontal cortex | 31 | 36 | −12 | 3.43 |
| | −29 | 3 | −12 | 3.74 |

**Table 3 | Results of the ROI analyses in the left and right anterior hippocampus to test for effects of conditional entropy.**

| Region | *t* | *df* | *p* (two-tailed) | Mean | *SD* |
|---|---|---|---|---|---|
| Right hippocampus | −0.23 | 14 | 0.82 | −0.05 | 0.85 |
| Left hippocampus | −0.86 | 14 | 0.40 | −0.15 | 0.66 |

**Table 4 | Results of the correlational analysis between participants' knowledge of the statistical structure and beta-values derived from hippocampal ROIs.**

| Region | Computer post-test | | | | Paper–pencil post-test | | | |
|---|---|---|---|---|---|---|---|---|
| | *t* | *df* | *p* (two-tailed) | *r* | *t* | *df* | *p* (two-tailed) | *r* |
| Right hippocampus | 3.80 | 13 | 0.002 | 0.73 | −0.30 | 11 | 0.772 | −0.09 |
| Left hippocampus | 2.22 | 13 | 0.045 | 0.52 | −1.02 | 11 | 0.331 | −0.29 |

while PMv was also significantly active when the goal of an action changed and temporo-occipital sites when changes of objects occurred. Thus, aIPS seems to be specifically sensitive to the compound of objects and their associated manipulations. It should be noticed that participants were instructed to answer questions regarding the used objects, rather than the different manipulations. Though we cannot conclude for sure that the observed effects relate to action observation rather than object observation, activation in the aIPS suggests that attention was nevertheless directed at the action step as a whole, instead of focusing on the objects alone.

Alternatively, the revealed effect of conditional surprisal could also be explained using the concept of expectation attenuation. Expectation attenuation describes a reduced neural response to an expected compared to an unexpected stimulus (Den Ouden et al., 2010; Todorovic and de Lange, 2012). It is comparable to effects of repetition suppression, but in contrast to this, it does not rely on direct repetitions of stimuli, but expectations based on memory. Our findings coincide also with results reported by Strange et al. (2005). The authors presented sequences of visual stimuli while participants had to respond to each stimulus by a corresponding button press. They found that activation in posterior fusiform gyrus and aIPS increased with increasing stimulus-induced surprisal. In contrast to the present study, the degree of surprisal in the study by Strange and coworkers depended on the overall probability of one stimulus to occur, i.e., its base-rate, and not on the current probability of a stimulus given the preceding one. Notably, since stimulus identity and required responses were not separated in the study by Strange and colleagues, their findings cannot clearly distinguish if the revealed neural response to stimuli with a higher surprisal reflects revision of prepared responses or revision of anticipated stimuli. In the present study, participants did neither have to respond to single action steps nor where they instructed to attend to the structure of the sequences. Higher activation of the aIPS for action steps with higher surprisal thus suggests that it also engages in predictive processes during passive observation of actions. Together, present findings and findings by Strange and colleagues indicate that the aIPS might be sensitive to the degree of surprisal in both dynamic as well as static visual sequences. Future work is needed to clarify if it is particularly sensitive to base-rate dependent surprisal of events, conditional surprisal, or both and how the effects are modulated by participants' task.

A possible alternative interpretation of activation patterns revealed by conditional surprisal in the present study would hold that it merely reflect visual processes. Possibly, participants used their knowledge of the most probable next object to focus their attention on it before action onset. In cases of surprising action steps, attention then would have to be withdrawn from the previously attended object and reoriented to the actually grasped one. Attentional reorienting, as for example necessary in the Posner paradigm, has been shown to correlate with activation in the superior temporal lobe and the inferior parietal cortex (Vossel et al., 2006). Accordingly, the correlation between conditional surprisal and aIPS activation may reflect attentional reorienting rather than revisal of anticipated action steps. However, this interpretation is unlikely for two reasons. Firstly, during all movie scenes presented in the current study, numerous exemplars of the different objects were concurrently visible, so that focusing attention on only one exemplar seems a highly implausible strategy. Secondly, the aIPS effect was specific for surprisal and did not overlap with any activation correlated with conditional entropy. If it would reflect necessity of attentional withdrawal, aIPS should be also modulated by the degree of conditional entropy, since conditional entropy describes how likely a shift of attention will be.

To sum up, finding activity in the aIPS to increase with a probabilistic mismatch between expected and observed action is in line with previous research showing it together with posterior temporal and premotor cortex to be activated when observed actions violate the observer's expectations (Schubotz and von Cramon, 2008; Schiffer et al., 2013) as well as when abstract visual stimuli elicit surprise (Strange et al., 2005; Bubic et al., 2011). The present results extend our knowledge on mechanisms underlying action observation by showing that expectations regarding upcoming action steps are constantly built and adapted during sequences of actions, even if not relevant for a task, and that the sensorimotor network is moreover sensitive to the strength of an observer's current expectations.

#### CONDITIONAL ENTROPY: PREDICTABILITY OF ACTION STEPS

Predictability can be viewed as the backdrop on which an occurring action step is processed. Thus, two action steps can be equally expected (in terms of their absolute probability), but for one action step, only one alternative action step exists (so that overall predictability is high) whereas for the other action step, several alternative action steps are concurrently possible (so that overall predictability is low). Accordingly, predictability is influenced by the number and the probabilities of all alternatives at a given point in an action.

We used conditional entropy to quantify action predictability, combining the number of possible action steps and their respective probabilities. Conditional entropy is the inverse of predictability, i.e., it is higher, the lower the predictability is. Several of our hypotheses, but not all, were confirmed by the data.

As expected, we found that high conditional entropy (and hence low predictability) of the next action step correlated positively with the BOLD response in the dmPFC, as well as anterior dorsal insulae, and lateral prefrontal cortex. Activation of the dmPFC, together with the anterior dorsal insula, is often found to increase during decision-making under uncertainty (Huettel et al., 2005; Volz et al., 2005; Preuschoff, 2008), also when uncertainty is unrelated to a possible outcome but affects a perceptual decision (Grinband et al., 2006; Summerfield et al., 2011). Uncertainty can be due to two factors; one is a lack of knowledge of the rules which describe the relation between events, also referred to as internally attributed uncertainty, the other is due to non-deterministic, i.e., probabilistic, relations between events, so that even when the rules which describe their relation are perfectly known, a perfect prediction of the upcoming event is not feasible. The latter type is also referred to as externally attributed uncertainty (Volz et al., 2005). Externally attributed uncertainty is induced by conditional entropy, as both rise as the number of possible events as well as the balance of their (reward) probability

increases (Hirsh et al., 2012). It has been proposed that anterior dorsal insula sub-serves a translation from unspecific drive states to concrete action plans when uncertainty is high (Wager and Feldman Barrett, 2004). For an actor, uncertain situations call for preparation of alternative actions and a flexible shifting between action plans. In the present study, we suggest that a similar coping strategy may apply to action observers: if conditional entropy of an upcoming action step was high, this led to recollection of the known alternative action steps and the readiness to flexibly shift between them in the course of action analysis, reflected in an increased BOLD response in anterior insula. Please note that since we only manipulated the degree of conditional entropy of the statistical structure underlying the action sequences and did not assess participants experienced uncertainty or asked them to engage in predictions, it remains speculative whether insular activation is an indicator of participants' feeling of uncertainty. We suggest that physiological processes associated with conscious coping with uncertainty (as, for example, during decision making) and those triggered by observing action steps with high conditional probability might partially overlap.

Notably, in contrast to our findings, Bornstein and Daw (2012) found a linear negative, not positive, relation between conditional entropy and activation in the anterior insula as well as the prefrontal cortex. Furthermore, Tobia et al. (2012) reported that the response profile of the insula to entropy could be best explained by a step-down function. That is, the authors found that insular activation was higher when entropy levels were within the lower 25% of the distribution of employed sequential entropy, and lower for medium to high entropy levels. No linear relation between entropy and insular activation was found.

The obvious discrepancy between these two studies reporting a negative relation between insular activity and stimulus entropy and our findings of a positive correlation calls for an explanation. An obvious difference can be identified in the learning stages at which participants were tested in the studies of Bornstein and Tobia, and ours: implicit knowledge of the statistical structure and hence the conditional entropy assigned to upcoming action steps was already established in the present study when participants entered the fMRI session and was kept stable throughout the whole sessions. Though we cannot exclude that participants continued learning about the statistical structure, the situation did not call for an acquirement of new knowledge about the underlying structure, but rather for further adjustments of the already existing knowledge. In contrast, the statistical structures had to be learnt online in the studies by Bornstein and Tobia and also changed during the experiment. Hence, whereas upcoming action steps in the present study were unpredictable solely because of the underlying statistical structure of the action sequences, upcoming stimuli in the two other studies were unpredictable because of two factors, the probabilistic nature of the underlying structure as well as lacking (implicit) knowledge about the nature of the structure itself. Further studies have to evaluate if this psychological difference caused the divergent response profiles in anterior dorsal insula.

In sum, our findings corroborate the role of dmPFC and anterior dorsal insula in situations of low predictability. Crucially, participants in the present study were not explicitly asked to engage in predictions nor was the statistical structure of the observed action relevant to the task. Modulations in dmPFC and anterior dorsal insula activity therefore show that prediction is an automatically triggered process during action observation. Moreover, statistically induced fluctuations of predictability do not have to become conscious to participants to modulate activation in dmPFC and anterior dorsal insula.

Based on previous findings (Strange et al., 2005; Harrison et al., 2006; Bornstein and Daw, 2012; Schiffer et al., 2012), we expected to find a positive correlation between the BOLD signal in the hippocampal formation and the conditional entropy assigned to the upcoming action step. Data did not support this hypothesis. However, we found *post-hoc* a correlation between the hippocampal beta-values and participants' familiarity with the statistical structure: the better participants had learnt the statistical structure, the stronger was the hippocampus positively correlated with the conditional entropy (i.e., the higher was the extracted beta-value). It has been proposed that correlation between hippocampal activation and predictability reflects retrieval of mental representations of possible events (Bornstein and Daw, 2012; Schiffer et al., 2012), such that hippocampal activity increases with the number (and hence unpredictability) of possible events. The revealed finding here suggests that this correlation depended on the degree of implicit knowledge participants had acquired. However, given the correlational nature, the data can also be interpreted differently. Possibly, the correlation between conditional entropy and hippocampal activation did not result from participants' higher familiarity with the statistical structure, but was a prerequisite for it.

Note that the considered correlation was only found for the computer post-test, but not for the paper–pencil post-test on statistical action knowledge. We suggest that the two post-tests engaged different processes. The computer post-test was closer to the experimental requirements during the training and the fMRI session, since participants were presented with a short video clip showing the succession of two action steps. Furthermore, probability judgments were assigned to the just presented transition and participants were not required to take the alternative transitions into account as in the paper–pencil post-test. Thus, participants may have reflected their judgments more in the paper–pencil post-test, making it a more explicit knowledge test, relying also on different memory systems.

A positive yet un-hypothesized correlation between activation of the right lOFC and conditional entropy was revealed. Increased activation in lOFC has previously been reported for inference of action goals based on manipulation information (Schubotz and von Cramon, 2008). The authors suggested that activation of the lOFC reflects increased demands on evaluating which of the expected action goals fits best with the observed manipulation. In close keeping with this interpretation, we assume that lOFC weighs information on currently possible action steps and their respective probabilities to lateral and medial PFC. According to Wallis (2007), dlPFC and dmPFC use this information to generate cost-benefit balanced behavioral plans. With the proceeding of the action step, further sources of information, as, e.g., motion signals, including trajectories, hand postures, or grip type become available. Due to its connections to sensory

areas, the OFC can integrate this information and provide this to dlPFC, further biasing the prediction of the action step (cf. Wallis, 2007). Accordingly, studies on decision-making report the lOFC for finding contingencies between stimulus-outcome associations (Rushworth et al., 2011) as well as for facing ambiguity, i.e., uncertainty due to missing information (Hsu et al., 2005). In these situations, further information, provided for instance by the reward history or somatic markers, has to be integrated to come to a decision (Bechara et al., 2000; Hsu et al., 2005; Mushtaq et al., 2011). Possibly, in the present study information on interoceptive states is provided by anterior dorsal insula (Craig, 2009).

Furthermore, we found activation in the pIPS to increase with conditional entropy. This activation points to altered attentional processes under low predictability. The pIPS belongs to the ventral frontoparietal network, as described by Corbetta and Shulman (2002). The authors proposed that the ventral frontoparietal network is particularly engaged in processing of previously unattended stimuli and hence reflects an orienting response to unexpected stimuli. Interestingly, we did not find activation in the pIPS modulated by conditional surprisal of an action step, but only by its conditional entropy. If conditional entropy is high, the likelihood of a necessary reorientation rises. We therefore speculate that activation of the pIPS in advance to necessary reorienting reflects a preparatory activation, dealing with the required flexibility of attention focus under high conditional entropy. This interpretation is in line with findings by Schubotz et al. (2012). In their study, activation of the posterior parietal cortex (more precisely, the posterior AG) was revealed when detection of action boundaries was contrasted with the detection of boundaries in intransitive (tai chi) movements. The authors suggest that at action boundaries, an exploration of potentially upcoming relevant aspects of the scene takes place and a shifting of attention to this spots is prepared, which is reflected in increased activation of posterior AG. We thus suggest that during action observation, participants' brains exploit scenes in anticipation of an upcoming reorientation of attention, resulting in a rise of activation in posterior parietal cortex.

To sum up, we found that conditional entropy of observed actions drew on areas known to be engaged during decision making under uncertainty, namely the dmPFC, anterior dorsal insula, and lOFC, as well as on the pIPS, an area that has been associated with shifts of attention. We suggest that pIPS reflects the preparation of potential shifts of attention when the further course of the action is rather unpredictable. Possibly, dmPFC, anterior dorsal insula, and lOFC show integration of additional information in order to enhance action prediction.

### FINAL REMARKS

The present fMRI study focused on the exploitation of the statistical structure in observed actions. We found that two characteristics can be distinguished with regard to their neural correlates. On the one hand, low predictability of action steps calls for a top-down modulation of attentional focus and stimulus processing, reflected in higher activation in a fronto-parietal network. On the other hand, low probability of an action step shows in a stronger accentuation of bottom-up signals provided by the stimulus, indicated by higher activation in parietal sites.

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## SUPPLEMENTARY MATERIAL

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## 3.2 Prefrontal cortex activation reflects efficient exploitation of higher-order statistical structure

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# Prefrontal cortex activation reflects efficient exploitation of higher-order statistical structure



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Title: Prefrontal cortex activation reflects efficient exploitation of higher-order statistical structure

Abbreviated title: Exploitation of 1st- and 2nd-order information

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Abstract

Since everyday actions are statistically structured, knowing which action a person has just completed allows predicting the likely next. Taking even more than the preceding action into account improves this predictability, but also causes higher processing costs. Using fMRI, we investigated whether observers exploit 2nd-order statistical regularities preferentially if information on possibly upcoming actions provided by 1st-order regularities is insufficient. We hypothesized that anterior prefrontal cortex balances whether or not 2nd-order information should be exploited. Participants watched videos of actions that were structured by 1st- and 2nd-order conditional probabilities. Information provided by the 1st and by the 2nd order was manipulated independently. BOLD activity in the action observation network was more attenuated the more information on upcoming actions was provided by 1st- order structure, reflecting expectation suppression for more predictable actions. Activation in posterior parietal sites decreased further with 2nd-order information, but increased in temporal areas. As expected, 2nd-order information was integrated more when less 1st-order information was provided, and this interaction was mediated by anterior prefrontal cortex (BA 10). Observers spontaneously use both the present and the preceding action to predict the upcoming action, and integrating the preceding action is enhanced when the present action is uninformative.

Keywords: action observation, anterior prefrontal cortex, BA 10, information theory, statistical learning

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1. Introduction

Humans use knowledge about structural regularities to shape their expectations about upcoming events (Bubic, von Cramon, & Schubotz, 2010; Friston & Kiebel, 2009; Kok, Brouwer, van Gerven, & de Lange, 2013; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Turk-Browne, Scholl, Johnson, & Chun, 2010). A good example of this ability is action observation: actions provide a conditional structure of sequential action steps so that knowing about a preceding action step improves predictability of the upcoming action (Zacks, Kurby, Eisenberg, & Haroutunian, 2011). Therefore, it appears that the more preceding action steps an observer takes into account, the more accurate the prediction will be. For instance, we do expect that a person will put a tea bag into a mug after switching on a kettle, but we do not if we observed that person putting a descaler into the kettle right before. Here, the 1st-order conditional probability of "putting a tea bag" after observing "switching on a kettle" is modulated by taking one additional action step into account, which constitutes a 2nd-order conditional probability. However, retrieving this 2nd-order information comes at processing costs, and might not always be worth it. Do observers always consider as many preceding action steps as possible to optimize their predictions, or do they only do so if their expectation is hardly informed by the directly preceding action? We know that humans do not take into account all available sources of information to come to an optimal decision, but often jump into solutions and take heuristic shortcuts (Gigerenzer & Goldstein, 1996). A basic question in human cognition concerns this cost-benefit ratio: How much information processing is invested (as a cost) to optimize expectations and behavior (as a benefit)?

Behavioral and functional MRI (fMRI) findings strongly suggest predictive mechanisms are engaged during action observation. Humans are particularly quick and accurate at recognizing actions, even if visual information is sparse (Blake & Shiffrar, 2007) or parts of the action are occluded (Stadler et al., 2011; Zacks et al., 2011). The so-called action observation network (AON), including premotor cortex, inferior parietal lobule, and posterior temporo-occipital regions (Caspers, Zilles, Laird, & Eickhoff, 2010) shows reduced activation for expected compared to unexpected actions (expectation suppression, see Kok et al. 2012; Summerfield & de Lange 2014; Summerfield et al. 2008). For instance, AON activation is attenuated by previous encounters of an action (Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013), successful inference of action goals (Wurm, Hrkać, Morikawa, & Schubotz, 2014), or predictive regularities between action steps (Ahlheim, Stadler, & Schubotz, 2014; Schubotz, Wurm, Wittmann, & von Cramon, 2014). This shows that the human brain exploits previous action steps to prepare for upcoming action steps. However, it is so far unknown how many previous action

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steps are considered to improve predictability, and whether this occurs as a function of the brain's current informational status.

In general, the predictability of an upcoming event depends on the degree of structure that underlies the event sequence, and knowledge of this structure allows for more accurate predictions. Using various paradigms and stimuli, it has been shown that humans spontaneously learn about 1st-order structures defined by conditional probabilities between successive stimuli, which can be accessed directly through pairwise associations. Humans use knowledge of those probabilities to prepare for upcoming stimuli, both among abstract stimulus sequences as well as actions (Ahlheim et al., 2014; Baldwin, Andersson, Saffran, & Meyer, 2008; Fiser & Aslin, 2002; Swallow & Zacks, 2008; Turk-Browne, Scholl, Chun, & Johnson, 2009). However, most everyday actions are not guided by simple 1st-order conditional probabilities, but involve higher-order (e.g., 2nd-order structures). Contrary to 1st-order information, 2nd-order information cannot be assessed directly, but requires retrieving information about the event *n-2* from memory, and integrating it with the 1st-order information. This integration is necessary, as the event *n-2* alone does not constitute the 2nd order, but only in combination with the event *n-1*. While the beneficial effects of 1st-order regularities on neural processing and behavior are uncontroversial, it remains unclear whether and how 2nd-order regularities influence behavior and prediction of upcoming events, and how this depends on concurrently available 1st-order information. Findings are mixed, as some fail to reveal an effect of higher-order structures (Gureckis & Love, 2010), while others show that learning of higher-order structures is slower (Remillard, 2008), or not different from 1st-order at all (Domenech & Dreher, 2010). Research in amnestic patients revealed a specific deficit in the learning of higher-order conditional structures (Curran, 1989). This suggests that the hippocampal formation, which is frequently damaged in amnesia, specifically contributes to learning of higher-order compared to lower-order structures, additionally to its critical role in episodic memory and associative knowledge (Fortin, Agster, & Eichenbaum, 2002; Kumaran & Maguire, 2009; Strange & Dolan, 2001).

In order to account for the mixed findings on learning of higher-order structures, it has been suggested that humans are biased towards attending to lower-order structures, and only attend to higher-order structures if the information provided by the lower-order structure is insufficient to reliably predict the upcoming event (Gureckis & Love, 2010). We suggest a similar effect in action observation. Recent findings indicate that the search and use for further information is orchestrated by the lateral BA 10 (Badre, Doll, Long, & Frank, 2012; Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006), an area that has furthermore been associated with the integration of different sources of information (Nee, Jahn, & Brown, 2013).

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In the present fMRI study, we tested the hypothesis that observers' exploitation of 2nd-order statistical information in action sequences depends on how much information was already provided by the 1st order. We used fMRI to test whether information from an observed action's 2nd-order statistical structure is used the more the less informative the action's 1st-order statistical structure is.

We presented observers with videos of action sequences structured by 1st- and 2nd-order conditional probabilities. That is, the probability of a given action step *n* was to a quantifiable amount determined by the preceding action step *n-1* (1st-order statistical structure) and to another amount by the combination of the preceding (*n-1*) and the last but one preceding action step *n-2* (2nd-order statistical structure). Importantly, the amount of information provided by 1st- and by 2nd-order structure was varied independently. This enabled us to estimate both effects independently and also their interaction. We modeled the BOLD effect at the beginning of action *n* as a function of the amount of information provided by the action *n-1* alone and by the combination of action *n-1* and *n-2*.

We expected three effects:

1) First, we expected to replicate findings from our previous studies (Ahlheim et al., 2014; Wurm et al., 2014), showing that facilitating the prediction of the upcoming action step leads to an attenuation of activity in the AON. The more informative action *n-1*, the better the prediction of the upcoming action *n*. Accordingly, we expected the BOLD response in the action observation network to decrease with the amount of information provided by action *n-1*.

2) At the same point in time, integrating information from action *n-2* with information from action *n-1* can effectively modulate expectations based on the relation between the actions *n-1* and *n,* and thereby increase predictability of action *n*. Unlike 1st-order information, 2nd-order information cannot be accessed through direct associations between stimuli, but requires action *n-2* to be retrieved from memory and integrated with action *n-1*. We expected memory retrieval to be reflected in the hippocampal formation, due to its role in episodic memory and, especially, learning of higher-order sequences (Curran, 1989; Fortin et al., 2002; Kumaran & Maguire, 2009; Strange & Dolan, 2001). We hypothesized that activation in the hippocampal formation will correlate positively with the amount of information provided by the 2nd order. Furthermore, we expected use of 2nd-order information to draw on the AON. Here, we considered two potential scenarios. First, given that the exploitation of 2nd-order information improves predictability of the upcoming action, it can be expected to result in a further attenuation of the AON, paralleling the effect of 1st-order information, and pointing towards an interpretation of AON activity as reflecting a gain in predictability. Alternatively, activation in the AON could

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also be expected to increase with the amount of 2nd-order information. This is because the more information is provided by the 2nd-order structure, the more the predictions based on the 1st-order change and thus, integrating 2nd-order information is more demanding. This pattern would point towards sensitivity of the AON to the integration costs of 2nd-order information with the previously provided 1st-order information.

3) Lastly, we were particularly interested in the question as to how exploitation of 2nd-order information depends on the amount of information already provided by the 1st-order – that is, which brain areas show a higher response to 2nd-order information when 1st-order is low compared to when it is high. We hypothesized that integration of 2nd-order information should be especially enhanced when action *n-1* alone was less informative about the upcoming action *n* and the need for further information is high. Thus, we expected a stronger modulation of the BOLD-signal by the 2nd-order information for trials with low compared to high 1st-order information. Due to its functional profile in exploitation and integration of information (Badre et al., 2012; Daw et al., 2006; Nee et al., 2013), we expected Brodmann Area 10 at the frontal pole to show the interaction effect of 1st- and 2nd-order statistical information.

## 2. Methods

### 2.1 Participants

Twenty-two healthy, right-handed participants volunteered for the study and were paid 80 € for their participation. The local ethics committee of the University of Münster approved the experimental protocol and written informed consent was obtained from each participant. Three participants had to be excluded after completing the experiment, one because of poor performance in the control task (score below two SD from mean), and two because of self-reported inattentiveness and sleep during the fMRI session. All following analyses are based on the data of the remaining 19 participants (mean age 25.35 ± 2.13 years, 14 females).

### 2.2 Stimuli and Task

We employed a paradigm that required constant monitoring of sequences of action steps that were structured by 1st- and 2nd-order conditional probabilities. To construct sequential actions devoid of semantic expectations, we used eight objects from the constructional toy Baufix® and defined the grasping and manipulation of an object as one action step. Overall, we created a total of 140 action sequences, ranging from four to nine action steps. Base-rate probability of occurrence was nearly identical for all action steps, ranging from 12% to 14%. Therefore, predictions of upcoming action steps could not reliably be based on frequency.

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To prevent participants from episodically remembering entire video clips as a basis for prediction we shot every sequence in seven versions, each with different starting scaffolds, which consisted of various different mounted objects (see Figure 1a for an illustration of the video clips).

Action videos were displayed on a grey background in the middle of a computer screen. A fixation circle with a duration of 3 s, or adjusted length after question trials, preceded all videos. Within the videos, onset asynchronies of the single action steps ranged from 1.28 s to 12.24 s (mean 4.39 s).

Approximately half of the video clips (64 of 140 during the training, 32 of 70 during the fMRI session) were followed by questions trials. Here, participants were required to answer questions concerning the previous video, e.g., "Has a long screw been used?". Responses were given via computer mouse with the right button (i.e., middle finger of the right hand) corresponding to the answer "no" and the left button (i.e., right index finger) corresponding to "yes". Half of the questions required a positive answer and all participants responded according to the same response contingencies. Questions were presented for 3 s or until the first response, and had to be answered within 3 s (see Figure 1a). The duration of the fixation circle following responses was adapted to compensate for different response times and could range from 2 to 5 s. Questions were followed by a feedback of 2 s indicating correct ("+"), incorrect ("-"), or delayed ("/") responses.

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2.2.1 Markov Matrix

The succession of action steps within the sequences followed pre-defined 1st- and 2nd-order conditional probabilities (see Figure 1b for an excerpt of the transition matrix). First-order conditional probability refers to the probability of each action step based on the immediately preceding action, ranging from 12.5% to 37.5% (rows 1-4 in the transition matrix, Figure 1b). The larger the difference between probabilities of the possible upcoming actions, the more information about the upcoming action was provided by the 1st-order structure. For instance, the blue cube provided more 1st-order information than the short screw, as it allowed for a better prediction of the upcoming action. Paralleling the 1st-order, the 2nd-order conditional probability refers to the probability of each action step based on the combination of the two preceding actions, ranging from 12.5% to 87.5% (rows 5-12 in the transition matrix, Figure 1b). Here, the larger the difference between probabilities of the possible upcoming actions, i.e., between all actions within one row of the matrix, the more information was provided by the 2nd-order structure. For instance, if a screw nut preceded the short screw, it provided much information on the upcoming action: the previously balanced probabilities on the 1st-order structure would become biased, and mounting the triangle would become the most likely action step. Contrary to that, a long

screw preceding the short screw provided little information, as the probability ratio between the next possible actions stays the same. As can be seen from the matrix, the amount of information provided by the 2nd-order structure varied independently of the information provided by the 1st-order structure. This feature of the statistical structure is important as it allowed us to test if the amount of information provided by the 1st order affects exploitation of the 2nd order as an additional source of information.

[insert Figure 1 here]

2.3 Experimental Procedure

Prior to the fMRI scan, each participant completed three 90-minute training sessions on three successive days to acquire implicit knowledge of the statistical structure. Since we wanted to test if human observers spontaneously attend to different levels of statistical structure, participants did not receive explicit learning instructions at any point either in training or during the fMRI session, and were not told that there was a certain systematic concerning the structure of the action sequences. Participants were familiarized with the eight different objects as well as with the type of question they would be asked before they started the training sessions.

The course of the fMRI session was identical to the training session, but no feedback was provided after question trials. To account for the limits in maximal duration of fMRI sessions, only 70 out of the 140 action sequences were presented, resulting in approximately 45 minutes of fMRI scan. The selected 70 sequences were a representative sample of the total set of sequences, while ensuring that rare action combinations (i.e. with low 1st- or 2nd-order conditional probabilities) occurred with sufficient frequency.

To test our prediction that participants would be capable of learning both 1st- and 2nd-order conditional probabilities, we implemented two post-scanner tests to assess participants' knowledge of the action syntax.

The first computer-based post-test was an serial reaction time task (SRTT, Nissen & Bullemer 1987) wherein pictures of the eight Baufix objects occurred at different locations on the screen. Unknown to the participants, the succession of the objects was defined by the same statistical structure as in the main experiment. Participants had to press a button, specifically assigned to each of the objects on an eight-button response pad as fast as possible. Wrong answers were followed by a negative feedback. This test was designed to test whether reaction times (RTs) would be modulated by both 1st- and 2nd-order conditional probability of the occurring object.

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The second post-test was a paper-pencil test. Eight video clips were presented in randomized order. Videos ended after the actor had used one object and reached for another. The participants' task was to mark those objects out of the set of eight that they expected to be used next and to weight them according to their respective probability. They made this judgment in the form of eight crosses, which they could assign among the eight objects. For instance, if participants saw a clip in which the long screw had been used and they expected the board and the screw nut afterwards with equal probabilities, they assigned four crosses to each of them. The number of eight crosses allowed participants to select up to all eight possible objects and to weigh them accurately (each cross corresponded to $p = .125$).

2.4 Data Acquisition

A 3T Siemens Magnetom Trio (Siemens, Erlangen, Germany) system equipped with a standard birdcage head coil was used in the functional imaging session. Participants lay supine in the scanner and their right hand was placed on a four-button response-box. Index and middle finger were placed on the response buttons and response contingencies were the same as in the training sessions. Participants' heads and arms were stabilized using form-fitting cushions, and earplugs were provided to attenuate scanner noise. The experiment was presented via a mirror that was built into the head coil and adjusted individually to provide a good view of the entire screen.

During the functional imaging, 28 axial slices (128.8 mm field of view, 4 mm thickness, 0.6 mm spacing; in-plane resolution of 3x3 mm) parallel to the bi-commissural line (AC-PC) were collected using a single-shot gradient echo-planar (EPI) sequence (2000 ms repetition time; echo time 30 ms, flip angle 90°, serial recording, 1260 repetitions) blood-oxygenation level-dependent (BOLD) contrast. After the functional imaging, 28 slices of anatomical T1-weighted MDEFT images (4 mm thickness, 0.6 mm spacing) were acquired.

High-resolution 3D T1-weighted whole brain MDEFT sequences (128 sagittal slices, 1 mm thickness) were recorded for each participant in a separate session for improved localization of activation foci. Functional data were offline motion-corrected using the Siemens motion protocol PACE (Siemens, Erlangen, Germany). Further processing was conducted with the LIPSIA software package, version 2.1 (Lohmann et al., 2001). To correct for temporal offsets between the slices acquired in one scan, a cubic-spline interpolation was used. To remove low-frequency signal changes and baseline drifts from the BOLD signal, we applied a high-pass filter of 1/89 – 1/70 Hz, defined by an algorithm implemented in the Lipsia software package. Functional data slices were aligned with a 3D stereotactic coordinate system. The matching parameters (six degrees of freedom, three

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rotational, three translational) of the T1-weighted 2D-MDEFT data onto the individual 3D-MDEFT reference set were calculated. These parameters were used in a transformation matrix for a rigid spatial registration, normalized to a standardized Talairach brain size (x = 135, y = 175, z = 120 mm; Talairach & Tournoux, 1988) by linear scaling. Thereafter the normalized transformation matrices were applied to the functional slices in order to transform them using trilinear interpolation and align them with the 3D-reference set in the stereotactic coordinate system. The spatial resolution of the resulting functional data was 3 mm * 3 mm * 3 mm (27 $mm^3$). A spatial Gaussian filter of 8 mm full width at half maximum (FWHM) was applied to the data.

2.5 Data Analyses

2.5.1 Information Theoretical Modeling

To operationalize the amount of information provided by the 1st and 2nd order, respectively, we used measures derived from information theory and an *ideal observer model* to estimate conditional probabilities of action steps (cf. Ahlheim et al. 2014; Bornstein & Daw 2012; Harrison et al. 2006; Strange et al. 2005). Therefore, simulated probabilities were calculated across the training session, and continued through the scanning session. The base probabilities ($p$) of single items were calculated as the number of occurrences $n$ of item $x_t$ divided by the sum of all items $x_i$ that have appeared so far (see equation 1). The addition of the value 1 shapes a Dirichlet function.

$$p(x_t) = \frac{n(x_t)+1}{\sum_i x_i + 1}$$

Equation 1. Calculation of probabilities.

The amount of information provided by an event can be quantified as the degree to which uncertainty about an upcoming event is reduced. Uncertainty can be represented as entropy (H) (Equation 2), which is higher when unexpected events are probable (Cover & Thomas, 1991; Shannon, 1948). Entropy is therefore also referred to as expected surprise. The surprise of an event is defined as the negative logarithm of its probability, i.e. the surprise of an event is higher if the event was less likely. Formally, entropy is maximal if all possible events are equally likely to occur, so that $p_{event} = 1/n_{events}$. On the 1st order, the entropy about possible upcoming events (members of X) after occurrence of one other event (member $x_{t-1}$ of all X) can be quantified as forward entropy (Ahlheim et al. 2014; Bornstein & Daw 2012, see Equation 3). If the forward entropy $H(X|x_{t-1})$ is

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smaller than the general entropy H(X), occurrence of $x_{t-1}$ provided information about the occurrence of X. This information $I_1$ can be quantified as the difference between the general entropy H(X) and the forward entropy (taking the preceding event into account, i.e., $H(X|x_{t-1})$). The same logic applies to information provided by the 2nd order $I_2$, which can be quantified as the difference between the 1st-order forward entropy $H(X| x_{t-1})$ and the 2nd-order forward entropy $H(X| x_{t-1}, x_{t-2})$ (Equation 4).

$$H(X) = \sum_i p\left(x_t^i\right) * \log p\left(x_t^i\right)$$

Equation 2. Calculation of the general entropy.

$$H\left(X|x_{t-1}\right) = -p\left(x_{t-1}\right)\sum_i p\left(x_t^i \mid x_{t-1}\right) * \log p\left(x_t^i \mid x_{t-1}\right)$$

Equation 3. Calculation of the 1st-order forward entropy.

$$H\left(X|x_{t-1}, x_{t-2}\right) = -p\left(x_{t-1}, x_{t-2}\right)\sum_i p\left(x_t^i \mid x_{t-1}, x_{t-2}\right) * \log p\left(x_t^i \mid x_{t-1}, x_{t-2}\right)$$

Equation 4. Calculation of the 2nd-order forward entropy.

2.5.2 fMRI Data analysis

For the statistical evaluation of the BOLD signal, a design matrix was generated modeling events with a delta (stick) function, convolved with the hemodynamic response function (gamma function; Glover 1999). All modeled actions had a minimal inter-stimulus-interval of 2 seconds. The first two actions of each sequence were discarded, as 2nd-order information was not available for those. The general linear model included five regressors, which were modeled time-locked to the onset of the action steps and with a duration of 1 s. Onset of action steps was defined as the moment the hand started to reach towards the next object. The first regressor served as a baseline and was modeled with an amplitude of 1.

To model information provided by the 1st order, we included a parametric regressor in which entries in the amplitude vector corresponded to the amount of information provided by the 1st order ($I_1$). Paralleling this account, we included another parametric regressor in which entries in the amplitude vector corresponded to the amount of information provided by the 2nd order ($I_2$). To assess whether exploitation of the 2nd-order information

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depended on whether the 1st-order structure provided more or less information, we constructed an additional parametric regressor which modeled only those events for which the amount of information provided by the 1st order fell within the 1st or 4th quartile of the distribution of information provided by the 1st order (lowest and highest 25%). The amplitude entries on this regressor corresponded to the interaction term of 1st- and 2nd-order information, calculated as their mean-centered product (see Figure 2a for an illustration for the course of the parametric regressors during an excerpt of the experiment).

In addition to the parameters modeling amount of provided information, we included the 1st-order conditional surprise, i.e., the negative logarithm of each action step's conditional probability, as a nuisance regressor. Amplitudes of all parametric regressors where separately z-scored for each participant.

To account for question trials and general effects of observing actions, we included question trials with a duration of 3 s and video clips with a duration according to the duration of the video, both with an amplitude of 1.

We corrected for multiple comparisons by applying a two-step correction approach, resulting in a correction at $p < .05$ at the cluster level. In the first step, an initial $z$-threshold of 2.57 ($p < .01$, two-tailed) was defined. All voxels showing activation above this threshold entered the second step of the correction. Here, a Monte Carlo simulation was used to define thresholds for cluster-size and cluster-value at a significance level of $p < .05$. The combination of cluster size and cluster value decreases the risk of neglecting true activations in small structures. Thus, all reported activations were significant at $p < .05$, corrected for multiple comparisons at the cluster level.

## 2.6 Behavioral Analysis of post-fMRI Tests

The behavioral analysis was conducted with the statistic software package R, version 3.1 (R Foundation for Statistical Computing, Vienna, Austria) and SPSS statistics version 22 (SPSS Inc. Chicago, Illinois, USA). If not indicated otherwise, all inferential decisions were based on an alpha level of .05.

### 2.6.1 SRTT Analysis

The first post-fMRI test, the SRTT, was designed to measure whether RTs were modulated by 1st- and 2nd-order conditional probability. This would provide evidence for implicit learning of the respective orders. To test for this, we conducted a multiple regression analysis separately for each participant, which included the predictors of 1st-order conditional probability and 2nd-order conditional probability (see Equation 1) as well as

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the trial number to control for general learning effects. Using multiple regressions enables us to identify how much each predictor contributes to the observed data in the context of the simultaneously available predictors. Only correct trials with an RT between 100 ms and 2000 ms were included in the analysis. On average, 7 % (45 of 651 trials) were excluded per participant. One participant had to be excluded due to excessively prolonged RTs ($z > 2$), resulting in 18 participants in the final analysis of the SRTT. To account for the non-normal distribution of the RT data, all RTs were logarithmized prior to analysis. For each participant, we gained one standardized regression coefficient that reflected how strongly their RTs were modulated by the 1st-order conditional probabilities, and one that reflected how strongly RTs were modulated by 2nd-order conditional probabilities, while controlling for effects of the respective other predictor. Those standardized regression coefficients were tested for significant deviation from zero, using separate one-sample t-tests (cf. Bornstein & Daw 2012 for a similar approach).

2.6.2 Paper-Pencil Analysis

The second post-fMRI test was a paper-pencil test where we assessed participants' explicit knowledge of the 1st-order structure. One participant failed to complete the post-test and was thus excluded from the analysis. We aggregated the number of crosses for the underlying true probability level (0, 12.5, 25, 37.5), for instance, how many crosses a participant distributed on average for a 0.25 conditional probability between action steps. This data was entered into a univariate ANOVA with the factor PROBABILITY (0, 0.125, 0.25, 0.375) to test for significant differences between the levels. To test for the expected increase of probability ratings with implemented probabilities, planned paired *t*-tests between the successive probability levels were conducted.

3. Results

Participants answered on average 26.4 out of 32 question trials correctly ($SD = 3.27$), indicating a high attentiveness during the fMRI session.

3.1 fMRI Results

Manipulating the amount of information provided by the 1st and 2nd order of the statistical structure independently of each other allowed us to assess functional correlates of the exploitation of each of the levels

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independently. Furthermore, it enabled us to investigate how the amount of information provided by the 1st order affects exploitation of further information provided by the 2nd order.

1) Effects of 1st-order information

The contrast testing for a modulation of the BOLD response by the amount of information provided by the 1st-order structure yielded an attenuation of activation in the predicted network of ventral premotor cortex (PMv), the midposterior part of the intraparietal sulcus (mIPS), and the fusiform gyrus and posterior middle temporal gyrus (pMTG), which is classically reported for action observation (see Table 1 for a list of all activations, Figure 2b). Since information provided by the 1st-order structure and information provided by the 2nd order were modeled simultaneously, this finding shows that increased predictability based on information provided by the 1st-order structure can reduce activation even when information from the 2nd-order structure is also available.

[insert Table 1 here]

2) Effects of 2nd-order information

Higher 2nd-order information was associated with a decrease of activation in mIPS, which overlapped with the cluster observed in the 1st-order contrast (1188 $mm^3$ in the left, 432 $mm^3$ in the right hemisphere; see Figure 2d for an overlay of the two contrasts). Furthermore, we found an increase in activation in pMTG, superior parieto-occipital cortex (SPOC), and the right temporal pole with amount of 2nd-order information (see Table 2 for a list of all activations, Figure 2c). Those findings show that 2nd-order information is spontaneously integrated, independent of 1st-order information.

To test for the hypothesized correlation between 2nd-order information and activation in the hippocampal formation reflecting effects for retrieval of 2nd-order information, we additionally conducted an ROI analysis in the anterior hippocampus. ROI coordinates were taken from a previous publication of our group (Ahlheim et al., 2014) and were based on reported effects of sensitivity of the hippocampus to entropy (Bornstein & Daw, 2012; Harrison et al., 2006; Strange et al., 2005). The center of the ROI in the left hippocampus was at x = −25, y = −16, z = −18, and the center of the ROI in the right anterior hippocampus was at x = 31,y = −17, z = −19. Both ROIs had a sphere with a radius of two adjacent voxels (6 mm). Neither ROI showed a significant modulation by 2nd-order information (all $p > .09$, Bonferroni-corrected alpha-level of .025).

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[insert Table 2 here]

3) 1st-order dependent exploitation of 2nd-order information

We hypothesized that exploitation of the 2nd-order information depends on the amount of information provided by the 1st-order structure. To test this, we included an interaction term modeling only those events for which the 1st-order structure provided least information (lowest 25% of the distribution) or the most information (uppermost 25% of the distribution). The interaction therefore reveals areas that were significantly more strongly modulated by information provided by the 2nd-order structure if the 1st-order structure provided only little information about the upcoming event. We found that activation in the PMd, the IPS, the precuneus, and the occipito-temporal lobe were more strongly modulated by information provided by the 2nd order of the statistical structure when less information was provided by the 1st-order structure.

Additionally, the interaction contrast yielded the predicted modulation of activity in lateral BA 10. BA 10 did not show a modulation by 2nd-order information or 1st-order information alone, which indicates that it is only modulated by information provided by the 2nd order if integration of this information was actually beneficial, i.e. when the 1st-order provided less information (see Table 3 for a list of all activations, Figure 2c). As can be seen from the bar chart in Figure 2c, this interaction effect was indeed driven by the cases in which 1st-order information was low.

[insert Table 3 here]

[insert Figure 2 here]

3.2 Behavioral Results

3.2.1 Results of the post-fMRI SRTT

The multiple regression testing for effects of the 1st-order and 2nd-order conditional probabilities on the logarithmized RTs revealed a significant negative relationship between 1st-order conditional probability and RTs, showing that higher 1st-order probabilities led to faster RTs ($t(17)= -6.92$, $p < .001$, two-tailed, $M= -0.12$, $SD= 0.07$ of the standardized coefficients). This effect was consistent across all participants. The effect of the

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2nd-order conditional probability was also significant ($t(17) = 2.37$, $p = .030$, two-tailed, $M = 0.03$, $SD = 0.06$), indicating slower RTs with higher 2nd-order probabilities (see Figure 3). Thirteen out of the 18 tested participants showed a positive correlation between 2nd-order conditional probabilities and RTs. As we conducted multiple regressions, those results show that RTs were slower for higher 2nd-order conditional probabilities whilst controlling for an effect of 1st-order conditional probabilities.

We furthermore wanted to test whether the effect of 2nd-order conditional probabilities depended on the degree to which expectations based on 1st-order conditional probabilities had been modulated by these 2nd-order conditional probabilities. To that end, we conducted a median split of the data for each participant, dividing trials by whether the 2nd order modulated the 1st order to a greater or lesser extent. We performed two multiple regressions parallel to the multiple regression described above, with 1st-order and 2nd-order conditional probability, as well as trial number, as predictors. The resulting standardized coefficients for the 2nd-order conditional probability depending on how strongly the 2nd order changed the expectations based on the 1st-order conditional probabilities were tested against each other using a paired $t$-test. A marginally significant difference was revealed ($t(17) = 2.04$, $p = .057$, two-sided). Thus, RTs showed a trend for being more strongly modulated by 2nd-order probabilities if those modulated the expectations based on 1st-order probabilities strongly ($M = 0.11$, $SD = 0.15$) compared to if the modulation was weak ($M = 0.03$, $SD = 0.11$; see Figure 3).

[insert Figure 3 here]

3.2.2 Results of the post-fMRI paper-pencil test

The results of the paper-pencil post-test, which assessed knowledge of the 1st-order structure, further corroborated the significant effect of 1st-order conditional probabilities on RTs. The repeated-measures ANOVA testing for an overall effect of the factor PROBABILITY on the assigned weight turned out significant ($F(3, 51) = 18.17$, $p < .001$, partial $\eta = .52$). As we expected rated probabilities to reflect actually implemented probabilities, planned paired $t$-tests were conducted between the single successive levels. We found no difference between probabilities of 0 and 0.125 ($t(17) = 1.61$, $p = .063$, one-tailed, $d = 0.38$), a marginally significant difference between probabilities of 0.125 and 0.25 ($t(17) = 2.09$, $p = .026$, one-tailed, $d = 0.49$) and a significant difference between 0.25 and 0.375 ($t(17) = 3.48$, $p = .002$, one-tailed, $d = 0.82$), with an alpha-level of .017, adjusted for the three comparisons (see Figure 4; note that the mean assigned values were scaled by the factor 12.5 to match the scaling of the implemented probabilities). This indicates that participants formed

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predictions based on the 1st-order conditional probabilities, and that their representation of 1st-order conditional probabilities was more precise for higher probability values. None of the participants claimed conscious knowledge of the structure when interviewed after the experiment.

[insert Figure 4 here]

## 4. Discussion

While it is well established that humans use predictive information in their environment to prepare for upcoming events, it is still unclear to what extent and under which conditions they do so is still. It is one of the currently most urgent questions how the brain selects the sources of information to generate predictions (Blokpoel, Kwisthout, & van Rooij, 2012; Phillips, 2013). The present study investigated whether information from an action's 2nd-order statistical structure is exploited in dependence on the information provided on the 1st level; in other words, whether the brain predicts upcoming actions in a cost-benefit ratio-optimized manner. We operationalized benefit as BOLD response decrease, and costs as increase.

Our results show that the brain exploits 1st- as well as 2nd-order statistical information, and that it does so in a cost-benefit shaped manner. Our findings are threefold: first, the information derived from the last action saves processing costs of the upcoming action. Second, at the same point in time, information from the last-but-one action is additionally exploited and facilitates the observer's predictions further. And finally, information derived from the last-but-one action is exploited more when the last action alone is less useful in shaping expectations.

### Attenuation in the action observation network based on 1st-order statistical information

In a first step, we sought to replicate and expand previous findings concerning the neural correlates of an increase in predictability by the 1st-order structure in action sequences (Ahlheim et al., 2014). We established in our behavioral post-tests that human observers learned 1st-order conditional probabilities and were particularly good at discriminating between action pairs of high conditional probability, even though no participant reported noticing those regularities in a post-experimental survey.

Previous studies reported that valid prediction of upcoming events leads to decreased activity levels in brain areas that code for these events, and that predictive information facilitates perception (Bar, 2004; den Ouden, Kok, & de Lange, 2012; Kok et al., 2012; Summerfield et al., 2008). We extended these findings to the

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case of action observation and found that an increase in the amount of 1st-order information led to the predicted attenuation of activity in the action observation network, composed of PMv, mIPS, and posterior temporal cortex (Caspers et al., 2010; Jeannerod, 2001). This shows that prediction of the upcoming action step was facilitated by information provided by the 1st-order structure. The established attenuation in this network adds to previous findings, showing that prediction-facilitating effects of 1st-order structure remain unaffected in the presence of a 2nd-order structure.

Integration of 2nd-order statistical information

To test whether human observers are capable of processing the 2nd-order conditional probabilities in our paradigm, we modeled the BOLD-response with a parametric regressor reflecting the amount of information provided by the 2nd-order structure. We found that activation of the mIPS decreased with the additional information provided by the 2nd order, on top of the decrease that mIPS showed as a function of 1st-order information. The mIPS was the only component of the AON that showed this pattern. The mIPS has been found to be a central focus of execution as well as observation of reaching movements (Vingerhoets, 2014). It is particularly interesting here that the mIPS area that we found is suggested to underlie the coupling of reaching and eye movements that is needed when we pursue visual hand input during reaching (Vesia & Crawford, 2012). Using temporal occluded targets during smooth pursuit eye movements, Lencer and co-workers (2004) found that this area bridges target occlusion, pointing to a role in anticipatory saccade tuning. Using 2nd-order information increases the predictability of the upcoming action step further, which allows for a more precise prediction of which object is going to be grasped next, and where this object can be found in the scene. The further attenuation of mIPS activation with 2nd-order information here reflects the further reduced processing costs of the upcoming reaching of the object, as target and direction of the reaching can be better predicted.

Contrary to 1st-order information, 2nd-order information could not be accessed directly through a pairwise association between action *n-2* and *n*. Instead, it was necessary to retrieve information about the action step *n-2* from memory and furthermore integrate this information with the information provided by the action *n-1* on the 1st order, as the action step at *n-2* alone was not informative of *n*. Notably, we found some evidence for retrieval costs in our post-fMRI SRTT: RTs increased with higher 2nd-order conditional probabilities whilst controlling for an effect of 1st-order conditional probabilities. Further, a trend-level effect ($p$= .057) tentatively suggests that this retrieval cost is higher, when 2nd-order information changed expectations based on the 1st-order conditional probabilities to a larger extent. Studies on learning of 2nd-order statistical regularities using a

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SRTT reported a decrease of RTs as reflection of statistical learning (Curran, 1989; Remillard, 2008). However, our SRTT differed in a critical point from a standard SRTT: Statistical regularities among the action steps were already established at the beginning of the testing, whereas the association between observed object and button press was not. How and when the retrieval costs of higher-order information begin to turn into a behavioral benefit thus needs to be explored further.

On the neural level, we expected that the retrieval of information about the action step *n-2*, which is necessary to asses 2nd-order information, would be reflected in an increased hippocampal activation with more 2nd-order information. Yet, using an ROI analysis, we did not find evidence for an increase of activation ($p > .09$) with increasing information provided by the 2nd-order structure in the hippocampus. We found, however, an increased activation in the right temporal pole, the more information was provided by the 2nd-order, as well as in the pMTG and the SPOC. The temporal pole is considered as "semantic hub" where semantic information about entities is processed, irrespective of their modality (Patterson, Nestor, & Rogers, 2007). In particular, it decodes conceptual object properties that go beyond the object's properties, as for instance the associated manipulation or the usual location of the object (Peelen & Caramazza, 2012). Furthermore, the temporal pole has been found to show a higher activation for initially biased perceptual decisions, and to pass this perceptual bias to visual areas (Summerfield & Koechlin, 2008). In the present study, higher 2nd-order information led to an increase in predictability of the upcoming action step and its associated object – in other words, the expectation of the upcoming action became more biased. This allows for a retrieval of semantic knowledge about the object – for instance, its shape or how it will be grasped and manipulated. We suggest that this retrieval of conceptual knowledge also drove the activation in the temporal pole in our study. Conceptual information is then passed to visual areas, i.e. the SPOC and pMTG. Area SPOC, at the mesial boundary between IPS and occipital lobe, is proposed to store internal representations of reach-to-grasp goals (Vesia & Crawford, 2012). We propose that here enhanced activation in SPOC reflects the maintenance of likely reach targets and their locations, which informs monitoring of the reaching movement in more parietal sites. Processing of this target, which is an object, is additionally enhanced in pMTG, which is a key-site of the processing man-made tools (Beauchamp & Martin, 2007). It should be noted though that we did not distinguish between different aspects of an action, that is the involved object and its manipulation. However, the amount of information provided by a certain object or action step varied depending on its position in the sequence, ensuring that the identity of the object itself could not be the cause of the effects revealed here.

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Evidence for information-state dependent use of 2nd-order information

To test the hypothesis that exploitation of the 2nd-order statistical structure depends on the amount of information provided by the 1st order, we conducted a parametric analysis for those events on which the 1st order was of very high or low informative value and tested for an interaction effect of 1st- and 2nd-order information. We found that activation in the PMd, the IPS, the pMTG, and the SPOC was more strongly modulated by the interaction term. Those areas, which have been described as the core areas of the AON (Caspes et al. 2010), were thus modulated more strongly by 2nd-order information when 1st-order information was low. This provides evidence for our initial assumption that higher-order information is preferentially used if 1st-order information is insufficient to generate precise predictions. We hypothesized that BA 10 orchestrates this cost-benefit trade-off. In line with our hypothesis, we found that lateral BA 10 was correlated with the interaction term. This correlation resulted from a stronger modulation of the BA 10 by the 2nd-order information if the 1st order provided only little information, i.e. if the action step *n-1* did not allow for a sufficiently precise prediction of action *n*. Crucially, of all the areas showing a sensitivity to the interaction contrast, BA 10 was the only area that was specific to the interaction of 1st- and 2nd-order information. This response profile corroborates our hypothesis that BA 10 contributes to a state-dependent integration of the 2nd-order structure. Across a variety of different paradigms, BA 10 has been reported to be activated when several relations among tasks or rules have to be integrated or organized (Golde, Cramon, & Schubotz, 2010; Koechlin & Hyafil, 2007; Nee et al., 2013; Ramnani & Owen, 2004; Schubotz, 2011). Here, and in line with findings from Golde et al. (2010), we showed that the BA 10 is also engaged when information derived from actions needs to be integrated. A particularly interesting parallel to our paradigm is the engagement of BA 10 in strategic exploration, when available cues provide insufficient information (Badre et al., 2012). Our results suggest that BA 10 may particularly contribute to a strategic retrieval of associations if these associations provide a clear gain in information. In other words, BA 10 may implement an efficiency criterion for the exploitation of higher-order information, presumably both in actions as well as in abstract stimuli.

Conclusion

The present findings provide several novel insights about the neurofunctional mechanisms underlying the prediction of observed action sequences. It shows that human observers spontaneously use both 1st- and 2nd-order statistical structure to predict upcoming actions, particularly when little information is provided by the 1st order. In particular, 1st-order statistical information in action sequences is automatically exploited and results in

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a faster and more efficient processing of the upcoming action step, manifesting in smaller RTs and a significant attenuation in the action observation network, respectively. Furthermore, information provided by the 2nd-order structure is retrieved and integrated to sharpen expectations, as indicated by activation increase in the temporal pole, and by attenuation in the IPS. Findings indicate that frontolateral BA 10 moderates integration of 2nd-order information, in line with the emerging understanding of this brain area as a hub for strategic integration of information from various sources.

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Table 1: MNI coordinates and maximal z-scores of significantly activated voxels for the parametric contrasts of information provided by the 1st-order structure

| Localization | MNI coordinates | | | *z*-values, local maxima | Cluster size ($mm^3$) |
|---|---|---|---|---|---|
| | x | y | z | | |
| ventral premotor cortex | -41 | 1 | 33 | -4.39 | 11691 |
| | 37 | 4 | 33 | -4.22 | 9855 |
| midposterior intraparietal sulcus | -17 | -62 | 48 | -3.99 | 8559 |
| | 25 | -53 | 42 | -3.38 | 1998 |
| midposterior intraparietal sulcus/ Precuneus | 13 | -65 | 54 | -2.87 | 567 |
| (BA 19) | 28 | -71 | 22 | -2.97 | 810 |
| Fusiform gyrus / | -50 | -59 | 0 | -3.96 | 6939 |
| posterior middle temporal gyrus | 40 | -50 | -21 | -3.06 | 1107 |

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Table 2: MNI coordinates and maximal z-scores of significantly activated voxels for the parametric contrast of information provided by the 2nd-order structure.

| Localization | MNI coordinates | | | *z*-values, local maxima | Cluster size ($mm^3$) |
|---|---|---|---|---|---|
| | x | y | z | | |
| dorsal premotor cortex | 28 | -11 | 54 | 3.82 | 4725 |
| local maximum in pCC | 7 | -12 | 39 | 3.58 | |
| midposterior intraparietal sulcus | -29 | -59 | 30 | -2.91 | 594 |
| | 25 | -50 | 36 | -3.31 | 3294 |
| posterior middle temporal gyrus | -50 | -68 | 18 | 3.11 | 405 |
| | 37 | -62 | 9 | 4.23 | 4455 |
| superior parieto-occipital cortex (BA 18) | -20 | -89 | 15 | 3.00 | 648 |
| | 16 | -92 | 21 | 4.56 | 13851 |
| Temporal pole | 52 | 4 | -30 | 3.50 | 4401 |

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Table 3: MNI coordinates and maximal z-scores of significantly activated voxels for the interaction contrast of information provided by the 2nd-order structure, depending on the amount of information provided by the 1st-order structure.

| Localization | | MNI coordinates | | | *z*-values, local maxima | Cluster size ($mm^3$) |
|---|---|---|---|---|---|---|
| | | x | y | z | | |
| anterior prefrontal cortex: | BA 10 | 32 | 52 | 9 | -3.23 | 5481 |
| | BA 11 | 14 | 50 | -15 | -3.82 | |
| dorsal premotor cortex | | -23 | -8 | 60 | -4.27 | 5076 |
| | | 22 | -2 | 57 | -3.72 | 4428 |
| Parietal and occipital lobe | intraparietal sulcus | -29 | -44 | 57 | -5.49 | 201285 |
| | | 33 | -40 | 56 | -4.68 | |
| | Precuneus | -9 | -62 | 68 | -4.90 | |
| | | 13 | -65 | 46 | -4.56 | |
| | superior parieto-occipital cortex | -15 | -101 | -6 | -5.20 | |
| | posterior middle temporal gyrus | -38 | -87 | -13 | -5.13 | |
| | | 39 | -70 | -17 | -4.47 | |
| Thalamus | | 16 | -26 | 12 | -4.00 | 1080 |
| Cerebellum | | 10 | -71 | -33 | -3.03 | 621 |
| Temporal pole | | 52 | 4 | -30 | 3.50 | 4401 |

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*Figure 1.* a) Illustration of the trial course. A fixation circle preceded each video and 46% of the videos were followed by a two-alternative forced choice question. Feedback on correctness of responses was only given during the training sessions. b) Excerpt of the employed transition matrix. Rows 1-4 show 1st-order conditional probabilities between action steps, rows 5-12 show 2nd-order conditional probabilities. Objects in rows depict the preceding objects of the transition. Red marked are two examples for possible 1st-order transitions with high or low information. Transitions with high information provided by the 1st-order structure are marked with criss-cross lines (red for 1st-order conditional probabilities, light or dark blue for 2nd-order conditional probabilities). Light blue fields show exemplary transitions with low, dark blue fields with high modulatory influence of the 2nd-order structure.

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*Figure 2.* a) Exemplary course of the parametric regressors for 1st-order information (red), 2nd-order information (blue), and their interaction term (black) during an excerpt of the experiment. b) Parametric effects of the amount of information provided by the 1st- order statistical structure. PMv: ventral premotor cortex, mIPS: midposterior intraparietal sulcus, pMTG: posterior middle temporal gyrus. c) Parametric effects of the amount of information provided by the 2nd- order statistical structure. mIPS: midposterior intraparietal sulcus, pMTG: posterior middle temporal gyrus, SPOC: superior parieto-occipital cortex, TempPole: temporal pole. d) Overlay of the parametric effects of the 1st- and 2nd-order statistical structure in observed action videos. Effects of 1st-order information are displayed in red, 2nd-order in blue. Effects of both parameters overlapped in the midposterior intraparietal sulcus (yellow) and comprised 1188mm$^3$ (59.46% of the activation cluster revealed in the 1st-order contrast) in the right and 432mm$^3$ (5.05%) in the left hemisphere. e) Interaction of parametric effects of the amount of information provided by the 2nd-order statistical structure and the amount of information provided by the 1st-order structure. The bar chart depicts beta-values in the BA 10 when the interaction term modeled only events with high 1st-order information (light blue, $t(18)= -0.18$, $p= .855$), low 1st-order information (dark blue, $t(18)= -3.12$, $p= .006$), and the interaction effect when events with high or low 1st-order information were modeled (middle blue, $t(18)= -3.41$, $p= .003$). pMTG: posterior middle temporal gyrus, IPS: intraparietal sulcus, preCun: precuneus.

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*Figure 3*. Results of the serial reaction time post-test. a) Mean beta weights expressing the relationship between 1st - and 2nd-order conditional probabilities and reaction times. Error bars depict ± 1 standard deviation. * $p < .05$, + $p < .06$.

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*Figure 4.* Results of the paper-pencil post-test, showing that assigned probabilities increased as implemented probabilities increased. Error bars depict ± 1 standard error. * $p < .017$, + $p < .03$.

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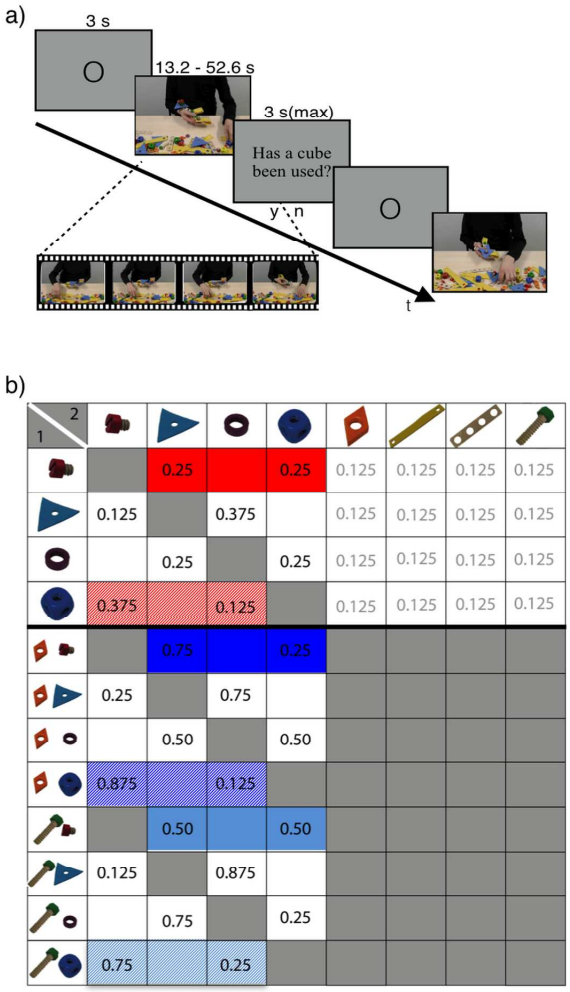


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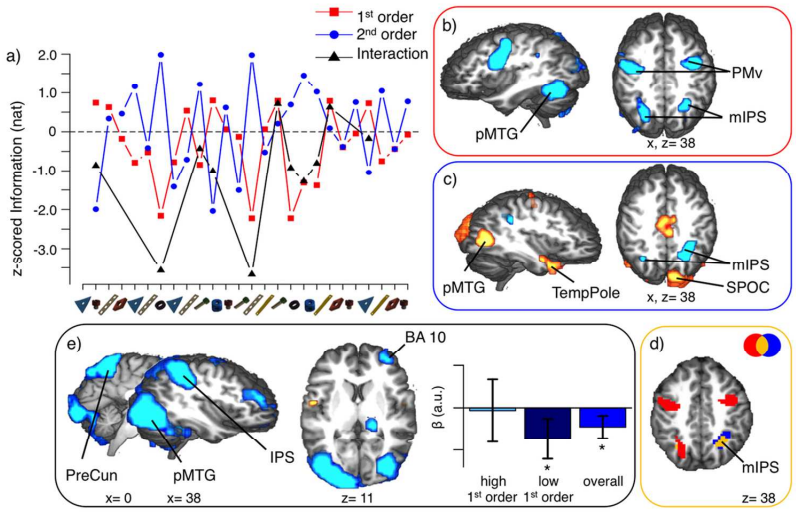


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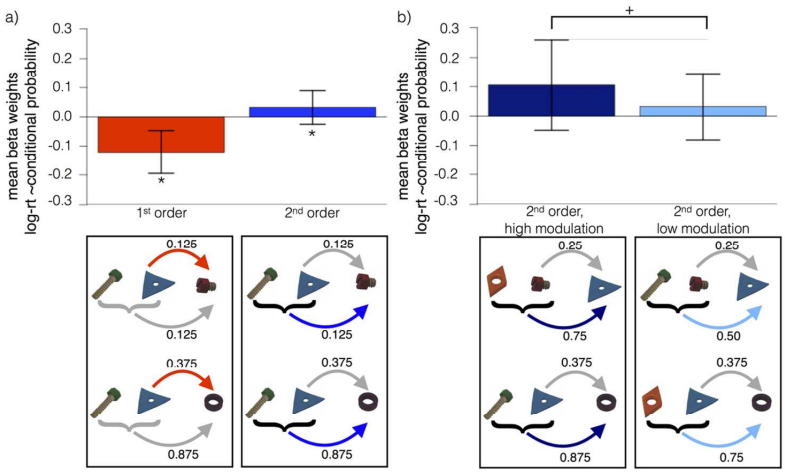


Figure 3. Results of the serial reaction time post-test. a) Mean beta weights expressing the relationship between 1st - and 2nd-order conditional probabilities and reaction times. Error bars depict ± 1 standard deviation. * p< .05, + p< .06.
116x70mm (300 x 300 DPI)

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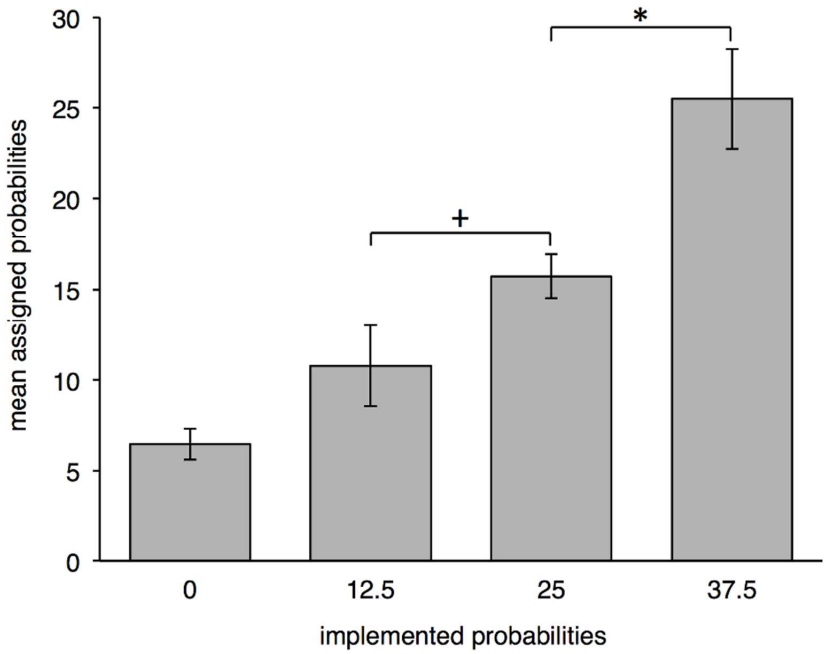


Figure 4. Results of the paper-pencil post-test, showing that assigned probabilities increased as implemented probabilities increased. Error bars depict ¬± 1 standard error. * p< .017, + p< .03.
80x64mm (300 x 300 DPI)

Only

## 3.3 Humans do not show use of an artificial event structure to predict observed actions

# Humans do not show use of an artificial event structure to predict observed actions

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**Abstract**

Humans are fairly good in predicting upcoming actions performed by others. Those predictions are based on many different sources of information and knowledge, including two aspects of an action's statistical structure: *sequential information*, capturing transitional probabilities between action steps; and *event information*, reflecting the structure of overarching events that observed action steps are part of. Although we know that such sources of information are available, it is unknown under which conditions human observers use them to predict observed actions.

We combined functional magnetic resonance imaging (fMRI) and behavioural modelling to test whether participants spontaneously use a complex event structure to improve their predictions of observed actions. The event structure could be derived from statistical associations among several action steps but not from preceding actions alone. Alternatively, only information derived from preceding action steps could be exploited for predictions, rendering predictions less accurate.

Participants were presented with successions of videos showing action steps that could be grouped together into distinct events and followed pre-defined transitional probabilities within those events. Neither behavioural nor fMRI results showed evidence for use of the event structure or transitional probabilities between action steps. A post-hoc fMRI analysis revealed that activation in posterior-temporal and intraparietal regions was modulated by an action step's frequency of occurrence in the recent past, showing higher activations for more remote action steps. This suggests that participants relied mostly on recency information. We discuss how specific features of the implemented event structure might have impeded its usage and put forward the idea that distinct transition states, referred to as bottlenecks, are critical for detection of event structures.

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**Introduction**

Humans can form accurate predictions of upcoming observations based on regularities in their environment. This is not only vital for successful behaviour (Fiser, Berkes, Orbán, & Lengyel, 2010; Wolpert & Flanagan, 2001), but has also been supposed to form a core mechanism of neural information processing (Clark, 2013). A prime example for human predictive capacities is provided by action observation: even if we do not actively engage in an action, but only observe it, we automatically predict which action step should be executed next (Ahlheim, Stadler, & Schubotz, 2014; Hrkać, Wurm, & Schubotz, 2014; Schubotz, Wurm, Wittmann, & von Cramon, 2014; Wurm, Hrkać, Morikawa, & Schubotz, 2014). How does the human brain achieve successful action prediction?

Actions can be described in terms of statistical structures which can be learnt through mechanisms of statistical learning (Baldwin, Andersson, Saffran, & Meyer, 2008; Baldwin & Baird, 2001; Buchsbaum, Griffiths, Plunkett, Gopnik, & Baldwin, 2014; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). Knowledge of the statistical structure can inform predictions of upcoming action steps in the absence of action knowledge, for instance an action's goal (Baldwin & Baird, 2001; Paulus et al., 2011). One aspect of an action's statistical structure is *event* information. Events reflect the grouping of separate action steps, that is, behavioural episodes that span multiple action steps (Zacks et al., 2007), for instance, *having breakfast* or *going to the dentist*. Information on distinct events covering succeeding action steps is captured by an *event structure*. If it is known which event a currently observed action is part of, next action steps can be more easily predicted (Csibra & Gergely, 2007).

In everyday life, events are commonly associated with an overarching goal that is achieved. This natural confound makes it difficult to disentangle effects of event knowledge and goal knowledge on action prediction (Buchsbaum et al., 2014). Experimentally, however, we can solve this problem by implementing *artificial event structures* devoid of semantic relations in order to investigate use of event structures during action prediction. It is largely unclear how human observers detect and use an event structure among succeeding action steps if no overarching goal

is known, and which brain regions are specifically sensitive towards event structures in observed actions.

Another source of information about a statistical structure is given by sequential probabilities among action steps. Behavioural and functional findings show that human observers implicitly use information derived from preceding actions in order to improve their prediction of an upcoming action (Ahlheim et al., 2014; Hrkać et al., 2014; Swallow & Zacks, 2008; Wurm et al., 2014). Thereby improved predictability of an upcoming action is reflected in an attenuation of activation in a network of posterior temporal, intraparietal, and premotor sites (Ahlheim et al., 2014; Wurm et al., 2014). This network is commonly referred to as action observation network (AON; see Caspers, Zilles, Laird, & Eickhoff, 2010).

These findings indicate that human observers are sensitive towards sequential regularities among action steps. However, it is unclear whether knowledge of an event structure can be acquired based on statistical regularities alone. An action's event structure goes beyond sequential regularities between action steps, and in order to optimize prediction of observed actions an event structure needs to be accounted for. This is because first, depending on the current event in which an observed action step appears, different action steps can be more likely to follow this action step. For instance, an egg can be cracked in order to prepare fried eggs or to bake a cake. Therefore, different action steps can be predicted after the egg has been cracked, in dependence of the current event. Second, events can be interrupted by other events. Interruptions suspend sequential regularities between action steps within an event (e.g. when someone answers the phone while baking a cake). If an interruption is observed, the observer needs to build a non-adjacent prediction (e.g. what will happen after the phone call). Hence, successful prediction of an upcoming action step should not be based exclusively on directly preceding action steps, but also take the current event into account.

Previous research investigating how humans distinguish events in a continuous stream of actions has focussed on the role of *prediction errors*, operationalized as low transitional probabilities, on the perception of events. It has been reported that groups of consecutive action

steps are perceived as events, despite no overarching goal was present (Avrahami & Kareev, 1994; Baldwin et al., 2008; Buchsbaum et al., 2014). However, a recent study challenges the assumption that event perception requires prediction errors (Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013). In this study, event perception was established among successions of abstract images. Crucially, transitions among images did not give rise to prediction errors. Instead, the perceived event structure resulted solely from the images' common temporal context (referred to as *temporal community*, a concept derived from graph theory, cf. Schapiro et al., 2013). Signatures of the event structure were revealed in the medial prefrontal cortex as well as the inferior frontal gyrus (Schapiro et al., 2013). Additionally, images that belonged to the same event became more similar in their representational pattern in the hippocampus proper (Schapiro, Turk-browne, Norman, Matthew, & Schapiro, 2016). This observation dovetails with previous studies reporting sensitivity of the hippocampus towards event structures (Davachi & DuBrow, 2015; Ezzyat & Davachi, 2014; Schapiro, Kustner, & Turk-Browne, 2012). A further study that investigated which areas are engaged in event detection in everyday actions revealed increased activation of the parahippocampal gyrus at the beginning of a new action event, compared to a midpoint of the event (Schubotz, Korb, Schiffer, Stadler, & von Cramon, 2012).

Here, we aimed to test whether human observers detect and use an event structure to improve their predictions of upcoming action steps. The event structure emerged from a common temporal context among action steps. A suboptimal prediction strategy would be to solely use information derived from preceding action steps. We presented participants with sequences of videos of action steps that could be grouped together to four distinct events. Each action step was part of two different events, so that the event identity could not be derived from a singly action step alone. Occasionally, events were interrupted by successions of event-unspecific action steps, that is, action steps that could interrupt any event and thus did not provide information on the evolving event. This allowed us to disentangle whether predictions of upcoming action steps were based on preceding actions or the underlying event structure. To assess the bases of participants' predictions, we modelled the neural response at an action step's onset in dependence of the

action's probability given either the event structure or one or two preceding action steps, respectively. Drawing on previous findings on improved predictability of actions (Ahlheim et al., 2014; Schubotz et al., 2014; Wurm et al., 2014), we expected a stronger attenuation of activation in the action observation network for predictions that reflected the event structure, compared to predictions based on one or two preceding action steps. Based on the crucial role of the hippocampus and surrounding structures in event perception, we further expected this area's activity to reflect use of an underlying event structure.

## Methods

### Participants

Twenty healthy, right-handed participants volunteered for the study and were either paid 30€ for their participation or received course credit. All participants had normal or corrected to normal vision and no history of medical, neurological, or psychiatric disorders or substance abuse. The local ethics committee of the University of Münster approved the experimental protocol and written informed consent was obtained from each participant. One participant had to be excluded after completing the experiment because of extensively prolonged reaction times during the fMRI session ($z > 2$). All following analyses are based on the data of the remaining 19 participants (mean age 24 ± 2.88 years, 8 male).

### Stimuli and Task

We presented participants with short video clips, each showing an actress picking up and mounting one single object of the constructional toy "Baufix" (referred to as one *action step*, hereafter). We used nine different objects and shot three versions of each action step, resulting in 27 different videos. Action videos were displayed on a grey background in the middle of a computer screen (see Figure 1 for an illustration of the video clips), and were separated by a 400 ms fading period. Duration of the videos ranged from 3.01 s to 7.00 s (mean 4.64 s).

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During the experiment, participants had to press a button corresponding to the colour of the object used in the presented video. To that end, objects were grouped together as *bluish* and *reddish* colours. Participants had to press the left button with their right index finger whenever one of the bluish objects was used (cube, triangle, disc, or long screw), and the right button with their middle finger when one of the reddish objects was used (board, short screw, band, cylinder, or screw nut), or vice versa. Participants were instructed to respond as quickly as possible when recognising which object was picked up. Irrespective of responses, videos always finished, and no feedback on the responses was given. Response contingencies were kept constant through the experiment for each participant and were balanced across participants.

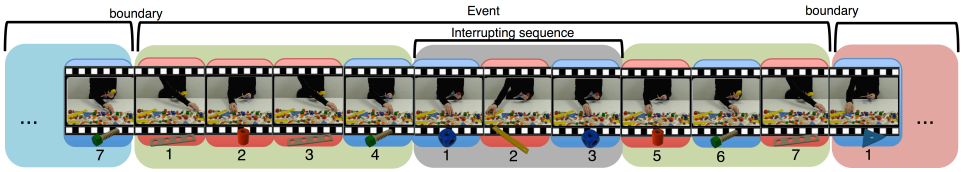


*Figure 1.* Illustration of the course of trials. Participants were presented with a continuous stream of separate video clips (each corresponding to a trial, here represented by video frames) and were instructed to respond for each clip whether the object picked was reddish or bluish (depicted by the coloured rectangles around each video frame for illustration purposes). Unknown to participants, succession of action steps was guided by an underlying event structure. One event (green background) involved seven videos (numbers below video frames) and events could be further interrupted (grey background) by distinct videos.

**Event structure**

To investigate whether events can be detected based on the temporal context of action steps, we developed an artificial event structure (see Figure 2). This event structure was the same for each participant, but concrete assignment from action steps (that is, objects) to positions in the event structure was counterbalanced across participants. Six of the nine action steps, *event actions* hereafter, constituted four different events, with each event containing three action steps, and each action step being part of two different events. Thus, all events shared one overlapping

action step, but no two events had more than one action step in common. Transition probabilities between event action steps were either 75% or 25%. In other words, within a certain event, the conditional probability of action step *t* given action step *t-1* was either 25% or 75%. Due to the overlap between events, it was not only necessary to know the action step *t-1*, but also to have information about the currently evolving event to know which possible two action steps could follow any specific action step. Each event sequence remained for seven action steps before a new event was entered. All transitions between events only contained transitions that could also occur within a sequence, i.e. had an event-specific 1$^{st}$-order conditional probability of either 25% or 75%. Thus, there was no prediction error in terms of 1$^{st}$-order transitional probabilities that could serve as a cue for changes of event. Transitions between the four events were also either 75% or 25%, and each event occurred 12 times throughout one session.

We furthermore included interruptions of the events that occurred in 50% of the presented events (24 in total). This allowed us to investigate whether human observers spontaneously use an underlying event structure to optimise predictions of upcoming action steps even if the current event cannot be derived from directly preceding action steps. Interruptions consisted of sequences with a length of three to five action steps that were not part of any event (actions 7-9), *interrupting actions* hereafter, thus not providing information on which event was currently evolving. Interruptions occurred with equal frequencies at any point after the second to fifth action step of a sequence. This ensured that the current event could be unambiguously identified before the interruption. For 2 of the 4 events, duration of the interruptions was fixed and was either three or five action steps long, whereas for the other two events the duration varied between three and five action steps, resulting in a mean interruption length of four action steps. Transition probabilities within the interrupting sequences were kept at 50%.

After an interruption, the previously evolving event continued at the position at which it had been interrupted. Thus, despite it was not known with certainty when the event would continue, it was possible to predict (based on the event-specific 1$^{st}$-order transitional probabilities) with which action step the event would continue. Additionally, we included eight long interrupting sequences

which were identical to the sequences that interrupted events, but occurred between instead of within events and unrolled for seven action steps, that is, with the same length as an event. This allowed us to balance baseline probabilities of all action steps.

Throughout the experiment, repetitions of action steps were prevented. Event actions each appeared 56 times, and interrupting actions appeared 50 to 52 times per session, resulting in a total number of 488 videos per session.

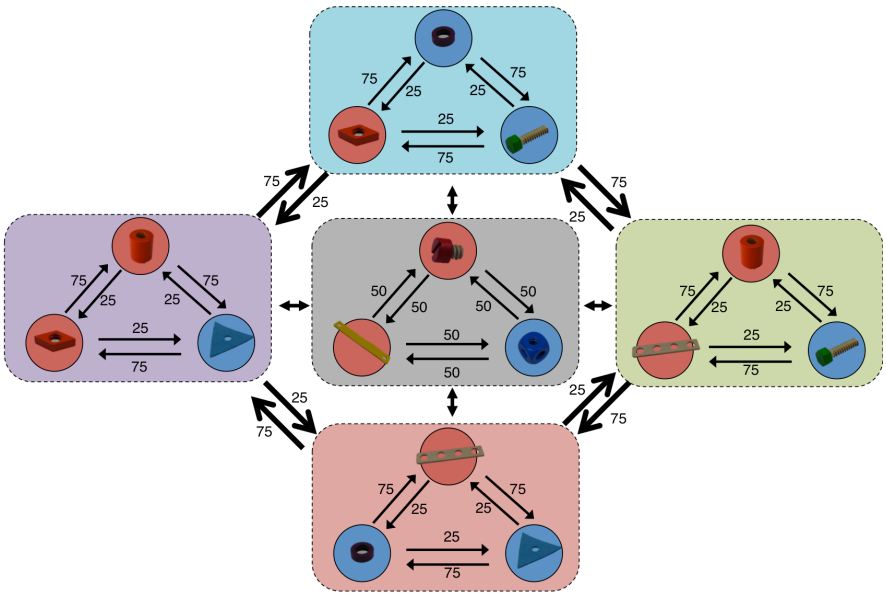


*Figure 2.* Illustration of the event structure. Four different events (indicated by coloured rectangles), composed of three action steps, were implemented in the experiment. Colour of circles around objects indicates the required response by participants (bluish or reddish). Transitional probabilities within events were either .25 or .75. Depicted in grey are interrupting actions, with transitional probabilities of .50. Interrupting actions could occur within any event, as indicated by bidirectional arrows.

**Experimental Procedure**

***Training and functional sessions***

Prior to the fMRI scan, each participant completed two 45-minutes training sessions on two successive days to acquire implicit knowledge of the event structure. We wanted to investigate whether event knowledge emerges spontaneously. To that end, participants did not receive explicit learning instructions at any point either in training or during the fMRI session and were not told that there was a certain systematic concerning the succession of the action steps. Participants were familiarised with the nine different objects and the required button press for each action step before they started the training sessions.

Videos were presented without any interruptions and no feedback regarding the button presses was given. During the training sessions, participants were given the possibility to take a break after approximately half of the experiment. No breaks were included in the fMRI session. Otherwise, course of the training and the fMRI sessions was identical. Different randomisations of the succession of action steps were used in each session and order of randomisations was balanced across participants.

***Post-fMRI test***

To test whether participants gained implicit knowledge of the event structure, we implemented a post-experimental test after the fMRI session. To that end, participants were presented with two triplets of action steps per trial (cf. Baldwin et al., 2008). On each trial, the two triplets differed only with regard to the last action step. Two different conditions were implemented with 18 trials each. The first condition tested for event knowledge. In trials belonging to this condition, one triplet consisted only of valid within-event transitions, and the other triplet showed transitions that did not occur within events, but were valid on the 1$^{st}$ order (i.e., triplets that could possibly occur between, but never within events). The other condition was conducted to test for sensitivity towards 1$^{st}$-order transitions. To that end, trials were composed of one triplet that

contained an illegal 1st-order transition between action steps and another triplet that consisted of only valid 1st-order transitions.

The two conditions were presented intermixed and presentation order of valid and invalid triplets within a trial was balanced across trials. Participants judged on each trial which of the two triplets has occurred more frequently during the fMRI session and were instructed to take as much time as they needed, but to rely on their gut feeling in case of doubt.

**Data Acquisition**

A 3T Siemens Magnetom Prisma MR tomograph (Siemens, Erlangen, Germany) with a 20 channel head coil was used for functional and structural data collection. Participants lay supine in the scanner and their right hand was placed on a two-button response-box. Index and middle finger were placed on the response buttons. Participants' heads and arms were stabilised using form-fitting cushions and earplugs were provided to attenuate scanner noise. The experiment was presented via a mirror that was built into the head coil and adjusted individually to provide a good view of the entire screen.

During the functional imaging, 30 axial slices (64 × 64 data acquisition matrix, 192 mm field of view, 4 mm thickness, 1 mm spacing; resulting voxel size of 3 × 3 × 5 mm) parallel to the bi-commissural line (AC-PC) were collected using a single-shot gradient echo-planar (EPI) sequence (2000 ms repetition time; echo time 30 ms, 90° flip angle, ascending recording, 1161 - 1200 repetitions) sensitive to blood-oxygen-level dependent (BOLD) contrast.

Prior to the functional imaging, high-resolution structural data were recorded for each participant using a standard Siemens 3D T1-weighted whole brain MPRAGE sequence (1 × 1 × 1 mm voxel size, 256 mm field of view, 192 sagittal slices, TR= 2130 ms, TE= 2.28 ms). SPM 12 (Wellcome Department of Cognitive Neurology, London, United Kingdom) was used for standard preprocessing and statistical analyses. In a first step, functional data were realigned for each participant. The participant's anatomical scan was then co-registered to the mean functional image

using a rigid-body transformation. Each participants co-registered anatomical scan was segmented, using probabilistic maps for grey matter, white matter, cerebro-spinal fluid, bone, soft tissue, and air/background, and was then normalised to the Montreal Neurological Institute (MNI) template brain. The thereby obtained parameters were applied to normalize functional scans to the MNI template. Functional images were resampled to a resolution of 4 × 4 × 4 mm voxels, and spatially smoothed with an 8 mm full-width half-maximum Gaussian kernel. XjView (http://www.alivelearn.net/xjview) was used to visualise the data.

**Data Analyses**

***Model definitions***

To test whether participants used the event structure or rather only one or two preceding action steps to inform their predictions of upcoming action steps, we generated parametric regressors reflecting each of the strategies.

To estimate probabilities of action steps, an ideal observer model was implemented (cf. Ahlheim et al., 2014; Bornstein & Daw, 2012; Harrison, Duggins, & Friston, 2006; Strange, Duggins, Penny, Dolan, & Friston, 2005). The base probabilities (*p*) of single items were calculated as the number of occurrences n of item $x_t$ divided by the sum of all items x (see equation 1). As those probabilities were already established during the training sessions, we implemented them as constant over the course of the fMRI experiment.

$$p(x_t) = \frac{n(x_t)}{\sum_i x_i} \qquad \text{(Eq. 1)}$$

In a similar vein, to test for effects of the 1st-order probabilities of an action, we calculated the 1st-order conditional probability $p(x_t|x_{t-1})$ across all trials. Likewise, 2nd-order conditional probabilities $p(x_t|x_{t-1}, x_{t-2})$ were calculated.

To assess event-based probabilities, we made use of the generative transitional probabilities for each action step specific to its current event $E_t$, that is $p(x_t|x_{t-1}, E_t)$, which could be either .25 or .75. From the event structure, it was not possible to make a certain prediction about which event would be interrupted and at which time. Thus, it was not possible to assign an event-based probability to the first action of an interruption, and those trials were accordingly not included in the analysis. All following actions of the interruption were assigned the probability of .50. Since interruptions varied in their length, it was not entirely predictable when the interrupted event would continue, but only with which action it should do so. Thus, the first event action after an interruption could not be reasonably modelled with its actual event-based probability, that is, .25 or .75. It was necessary to take the uncertainty as to whether the interruption continues or the event resumes into account. To approximate this, we divided the initially assigned transitional probability by two, resulting in probabilities of either .125 or .375. This approach implicitly assumes that participants expected the interruption to end with a constant probability irrespective of its passed duration.

Furthermore, the event structure did not allow for strong predictions of which action step would be observed when a new event started. This is because it was either possible to observe any action step of two different possible events, or to observe an action step belonging to a long interruption sequence. Thus, participants could have expected any of the eight remaining action steps (as repetitions of actions were excluded). Accordingly, we assigned a probability of 1/8 = .125 to the first action of a new event.

To take into consideration that probabilities are naturally bounded between 0 and 1, we calculated the respective surprise values for each of the parameters, defined as the negative logarithm of an observation's probability (Shannon, 1948).

As a by-product of the implemented event structure, the same action steps were presented repeatedly within one event, but were not presented outside their respective events. Thus, a possible heuristic to predict the upcoming action step could simply be the time since a respective action step was seen last. To control for this, we constructed an additional regressor that reflected how often a specific action step was seen in the recent past, hereafter referred to as *trace strength*,

based on a computational model (Balaguer, Tickle, & Summerfield, 2015). An action's trace strength was calculated for each trial. At the beginning, each action is assigned a trace strength of $s_i = 0$. When a particular action *i* is presented on a trial, its corresponding trace strength $s_i$ is updated using a delta rule with scalar learning rate α

$$s_i \leftarrow s_i + (1-s_i) \cdot \alpha \quad \text{(Eq. 2)}$$

On each trial, before any updating, the trace strength of all n actions $s_{1...n}$ is subject to a decay, controlled by a leak parameter $\gamma_i$

$$s_i \leftarrow s_i \cdot \gamma_i, \text{ for all } i \quad \text{(Eq. 3)}$$

As the trace strength was, like probabilities, bounded between 0 and 1, we used the negative logarithm of the trace strength. The trace model was fitted to each participant's reaction time data by maximising the correlation between the negative logarithm of the trace strength and mean-centred reaction times and exhaustively searching the best parameters through a grid. Possible values for α and γ ranged from 0 to 1 with steps of 0.05 (21 values per parameter in total), and the parameter combination that provided the best fit for each participant's reaction time data was used to model the fMRI data.

***Behavioural analysis***

All behavioural analyses were conducted in Matlab and inferential decisions were based on an alpha level of .05, if not specified otherwise.

*fMRI session*

As a behavioural measurement during the fMRI session, we collected reaction times for the bluish/reddish decision, as well as proportion of correct responses. Only correct responses with a reaction time between 500 and 4000 ms were included in the analysis. First, reaction times were mean-centred individually for participants and videos. This was done to take into consideration that the point when an object was picked up varied across the 27 different videos, and to further control for different response strategies participants might have used.

Reflection of event-based probabilities

In a first set of analyses, we aimed at testing for general effects of the implemented event structure. To this end, mean reaction times of action steps were calculated separately for the two within-event probability levels (.25 and .75) for each participant. Actions that occurred at event boundaries or during an interruption were excluded from the analysis. Mean reaction times were tested for difference using a paired *t*-test.

Model comparison

To test whether mean-centred reaction times were best explained by 1st-order surprise, 2nd-order surprise, event surprise, or the negative logarithm of the trace strength, we conducted a multiple regression analysis. As described before, the trace model contained two free parameters that were fitted to participants' behavioural data. Due to the serial dependence of the trials, it was not possible to perform a cross-validation within participants. We choose a leave-one-out approach across participants: each participant's behavioural data were modelled using the parameters that were derived from fitting the trace model to the data of all respective other participants. This fitting procedure did not control for individual differences across participants, and instead assumed that the best combination of parameters for each participant could be approximated by that of the rest of the sample. The GLM was run separately for all participants and resulting standardised beta coefficients were tested in separate one-sample *t*-tests for a significant deviation from zero.

*Post-test*

To assess whether participants' judgements accorded to the actual triplet frequencies, we aggregated each participant's correct responses separately for the two conditions (valid event vs. valid 1st order). The aggregated judgements were tested for a significant deviation from .50 (that is, chance level) using separate one-sample *t*-tests.

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***fMRI analysis***

A general linear model (GLM) approach was used to test whether brain activation was best explained by 1st-order surprise, 2nd-order surprise, event-based surprises, or the negative logarithm of the trace strength of action steps. The first five volumes of each participant were discarded from the analysis to allow the tissue to reach a steady state of radiofrequency excitation. A 128-s temporal high-pass filer was applied to remove low-frequency scanner artefacts from the BOLD signal. Temporal autocorrelation in the BOLD signal was estimated using a first-order autoregressive model (AR-1), and maximum-likelihood estimates of the activations were formed using the resulting non-sphericity, consistent with standard approaches in SPM (Penny, Friston, Ashburner, Kiebel, & Nichols, 2011).

In the GLM, only trials for which all of the separate regressors provided a value were modelled. We modelled each action step in an event-related fashion with the onset time-locked to the video onset and the duration according to the video duration. The GLM contained five regressors: the first regressor modelled each trial with an amplitude of 1 to capture any main effects of the video onset. We further included four parametric regressors testing whether the BOLD signal was best explained by 1st-order surprise, 2nd-order surprise, event-based surprises, or the negative logarithm of the trace strength. Each regressor modelled each trial with an amplitude corresponding to its value for the respective trial. Additionally, six regressors derived from the motion correction were included as covariates.

The resulting single-subject contrast images were entered into a second-level random effects analysis. For each contrast of interest, a one-sample *t*-test was used to test for significant deviation from zero. To control for false positives due to multiple comparisons, a family-wise error rate (FWE) correction was applied with a cluster threshold of $p < .05$ on the basis of voxel-wise threshold of $p < .001$.

## Results

### Behavioural results

#### *fMRI*

On average, participants answered 95% of the trials correctly, indicating high level of attentiveness. On average, two trials had to be excluded per participant due to premature (less than 500 ms) or prolonged (more than 4000 ms) reaction times (39 trials in total).

*Reflection of event-based probabilities*

Comparing mean-centred reaction times towards action steps that occurred with an event-based probability of .25 with action steps occurring with an event-based probability of .75 did not yield any significant difference ($t(18)= -0.98$, $p= 0.340$, $d= 0.23$, $M_{25}= -9.97$, $M_{75}= -0.30$, $SD_{diff} = 42.92$). Thus, we failed to find evidence that participants made use of event-based probabilities to prepare their responses.

*Model comparison*

To examine which structural information participants used to prepare for upcoming action steps, a multiple regression analysis was conducted, using the regressors of 1st-order surprise, 2nd-order surprise, event-surprise, and the trace strength. Averaged across all participants, only the trace strength showed a significant effect on reaction times ($t(18)= 6.06$, $p< .001$, $d= 1.39$, $M_{beta}= 0.10$, $SD= 0.07$; all other $p> .10$, see Figure 3). This provides further support for the finding that participants did not rely on event-based probabilities. Neither did participants' reaction times seem to be influenced by 1st- or 2nd-order surprise.

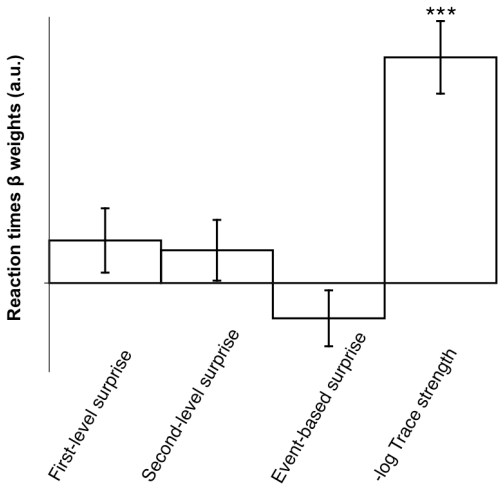


*Figure 3:* Average beta weights of the single subject multiple regressions, testing for an effect of 1st-order surprise, 2nd-order surprise, event surprise, or the negative logarithm of the trace strength on reaction times during the fMRI session. Only the trace strength showed a significant influence on reaction times across all participants.

**Post-test**

The hypothesis that participants judge within-event triplets as more frequent than triplets that did not occur within events could not be corroborated here. Instead, we found that participants judged within-event triplets as significantly less frequent ($t(18)= -3.13$, $p= .006$, $d= .75$, $M= 0.41$, $SD= 0.12$). A *post hoc* inspection of the data revealed that event triplets of the type *ABA* presumably drove this effect as those deviated most strongly from chance ($M= 0.35$). The one-sample *t*-test over trials that required a judgment based on 1st-order transitional probabilities did not reveal any significant results ($t(18)= -0.76$, $p= .457$, $d= 0.17$, $M= 0.47$, $SD= 0.18$).

**fMRI results**

Neither the contrasts of 1st-order surprise, 2nd-order surprise, nor event surprise revealed any significant activation. For the negative logarithm of the trace strength, three clusters survived correction for multiple comparisons. Those were bilaterally in the posterior middle temporal gyrus

(pMTG), extending into the fusiform gyrus, as well as the left middle intraparietal sulcus (mIPS; see Table 1, Figure 4).

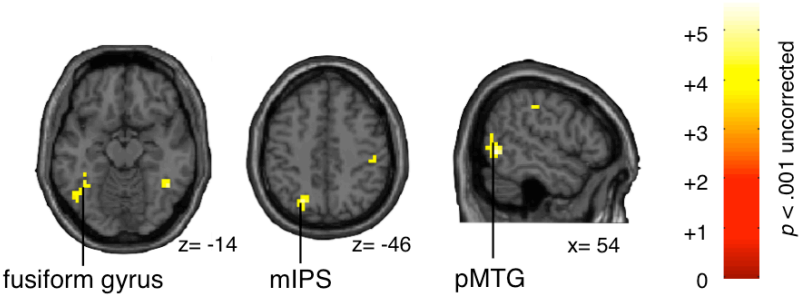


*Figure 4*: Areas showing a correlation with the negative logarithm of the trace strength ($p < .001$, uncorrected). mIPS: middle intraparietal sulcus; pMTG: posterior middle temporal gyrus.

*Table 1.* MNI coordinates and local maxima of clusters showing a significant correlation with the negative logarithm of an action's trace strength. Significant clusters survived FWE correction with a cluster threshold of $p < .05$ on the basis of voxel-wise threshold of $p < .001$.

| | MNI coordinates | | | cluster *p* | Cluster extent | Local maxima |
|---|---|---|---|---|---|---|
| | x | y | z | | (voxels) | (z) |
| middle intraparietal sulcus | -22 | -64 | 38 | .006 | 39 | 4.21 |
| posterior middle temporal gyrus | -46 | -64 | -2 | .001 | 54 | 4.09 |
| Fusiform gyrus | -38 | -44 | -18 | | | 3.62 |
| posterior inferior temporal gyrus | -46 | -60 | -10 | | | 3.55 |
| posterior middle temporal gyrus | 54 | -64 | -2 | .001 | 53 | 4.07 |
| posterior inferior temporal gyrus | 46 | -72 | -10 | | | 3.73 |
| | 42 | -76 | 2 | | | 3.48 |

## Discussion

When predicting observed actions, we can base our predictions on different aspects of an action's statistical structure. First, predictions can be based on sequential information derived from preceding actions. Second, information derived from an event structure can be used, that is, which overarching event is currently evolving. However, it is still unknown which kind of structural information human observers exploit preferably when predicting upcoming actions, and which features are mandatory for use of an event structure among succeeding action steps.

Here, we aimed to test whether human observers spontaneously use an event structure when predicting upcoming action steps even when the event structure cannot be derived with certainty through preceding action steps alone. Alternatively, it was possible that participants would not exploit the event structure, and instead solely rely on sequential information derived from a limited number of preceding action steps (i.e., $1^{st}$- or $2^{nd}$-order transitional probabilities). We designed a task where predictions of upcoming actions could be either made by (i) relying only on the directly preceding action steps, or (ii) taking also the identity of the current event into account that should even span across an interruption of the respective event. To test which strategy participants employed, we combined behavioural modelling and fMRI.

Surprisingly, we did not find evidence for participants exploiting transitional probabilities to predict upcoming action steps. This is in contrast to previous studies employing similar actions, where we showed that human observers spontaneously exploit information on upcoming action steps derived from one or two preceding action steps (Ahlheim, Schiffer, & Schubotz, 2015; Ahlheim et al., 2014). These former results extended findings by studies suggesting sensitivity to sequential regularities among abstract shapes (Domenech & Dreher, 2010; Harrison et al., 2006; Strange et al., 2005), pictures (Bornstein & Daw, 2012; Turk-Browne, Scholl, Johnson, & Chun, 2010), or tones (Nastase, Iacovella, & Hasson, 2014; Paraskevopoulos, Kuchenbuch, Herholz, & Pantev, 2012). We first discuss reasons for the unsuccessful replication of previous results before turning to *post hoc* findings.

Speculating on possible reasons for the replication failure, we suggest that the implemented transitional probabilities in the present study did not vary strongly enough. In contrast to our previous studies where the 1st-order transitional probabilities ranged from .25 to 1.0 (Ahlheim et al., 2014), most of them ranged only from .125 to .375 in the current study. Furthermore, tracking transitional probabilities was more difficult than in previous studies for two reasons: 1) the set of actions spanned nine different action steps, and 2) each action showed considerably strong transitional probabilities to four other actions.

We also did not find evidence for the use of the implemented event structure. We expected that exploitation of the event structure would lead to decreased reaction times for more likely action steps and to an attenuation of BOLD activation in premotor, parietal and posterior-temporal sites. Neither behavioural nor fMRI data showed an effect of event-based probabilities. Until now, only a limited number of studies have investigated how event perception emerges across sequences of action steps (Avrahami & Kareev, 1994; Baldwin et al., 2008; Buchsbaum et al., 2014), and no study has addressed how an event structure affects the neural processing of observed actions. Human sensitivity towards complex, multi-level structure has attracted strong attention in the domain of language (for a review, see Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015), but also in paradigms investigating human ability to strategically organize actions to accomplish multi-step tasks (Diuk et al., 2013; Solway et al., 2014). In language and in multi-step tasks it is necessary to identify the underlying structure, or hierarchy, of a series of observations. Critically, most studies investigating identification of hierarchical structures have employed unambiguous sets of items or steps, also referred to as clusters. This means that most single items were part of only one cluster, with only critical items connecting clusters, i.e. functioning as *bottlenecks* (Diuk et al., 2013; Solway et al., 2014). Contrary to that, in the present study, each action was part of two events and events could start with any action. These two factors both diluted the boundaries between events and thus might have impeded use of the event structure. We chose this approach to account for the ambiguity that we also face in everyday events: the same action step can be part

of potentially many different events and events do not need to start with the same action step to be recognizable for us.

Bottleneck states as pre-requisite for use of event structures

The present study built on a recent finding showing that event perception can emerge from a common temporal context, even in the absence of prediction errors (Schapiro et al., 2013). A feature of the structure implemented by Schapiro and colleagues was that the respective temporal contexts were connected via bottleneck states. Bottlenecks describe a specific feature of an environment, that is, states after which a particularly high number of different states can be reached (Diuk et al., 2013). This relates to the notion of connector hubs. Notably, bottlenecks do not need to be associated with prediction errors or an increased uncertainty (Schapiro et al., 2013). It has been shown that humans spontaneously identify and use bottleneck states in planning of multi-step actions (Diuk et al., 2013; Solway et al., 2014). Here, bottlenecks mark necessary sub-goals that need to be reached for successful performance (Botvinick, Niv, & Barto, 2009). In close notion with this, sub-goals in action sequences are considered as points that are mandatory in order to reach an overarching goal (Byrne & Russon, 1998). The relation between bottlenecks and sub-goals suggests that in observed action events, bottlenecks can be a cue for the completion of an event (and the beginning of a new one). In light of the findings by Schapiro and colleagues (2013), the present findings indicate that a common temporal context alone might not be sufficient to establish an event structure but suggest a critical role of bottlenecks between events.

In previous studies that successfully established an event structure among actions, participants' detection of the event structure was furthermore aided by constant event progression (Avrahami & Kareev, 1994; Baldwin et al., 2008), i.e. events spanned the same number of actions steps each time. In the present study, events were occasionally interrupted to allow us to test for the use of event knowledge beyond serial information, and thus events had variable subjective lengths. The interruptions lead to different dwell times within one event, thus not allowing using progression information as a cue for event perception. Participants might have exploited the event

structure if events had not been interrupted. However, findings on event emergence among abstract stimuli show that constant event progression is not mandatory for event perception (Schapiro et al., 2013). Event progression can possibly be rather interpreted as a cue that can aid event perception. Further research is needed to clarify the respective roles of bottleneck states, event ambiguity, and event progression for the use of event structures among action steps.

Post hoc finding: reflection of an action's trace strength in object sensitive areas

Apparently, participants exploited a feature inherent to the stream of action steps: resulting from our implemented event structure, the same three action steps re-appeared multiple times over a short period within a certain event, which led to a high local probability of occurrence. With a change of the event, this probability dropped for two of the three actions, and two other actions became likely. The probability remained high for the action step that overlapped between the two successive events. Local probabilities of action steps composing one event also dropped with the interruption of the event, thus rendering reliance on them suboptimal. It was possible that participants used local probabilities of action steps as a proxy to prepare for upcoming action steps instead of detecting the actual implemented event structure. We tested whether participants made use of local probabilities in our task by employing a *trace model*: here, the strength of the trace of each action step tracked how often that action step had occurred in the recent past, and varied in dependence of two parameters: The first parameter reflected the recency effect through a decay rate. In other words, it quantified how much the trace was weakened with each trial that the action step was not presented. The second parameter reflected the reinforcement of the trace, that is, how much it got strengthened each time the action step occurred. Both fMRI and behavioural data were best explained by this trace model. Notably, this finding was *post hoc*; we did not design the task with the aim of manipulating the strength of an action's trace, but rather found this as a by-product of the implemented event structure. Nevertheless, the finding is potentially interesting, as it offers an alternative mechanism that participants used to adapt to the present environmental structure.

If a specific action step was presented more often over a period of time, that is, its trace got strengthened, it became easier to recognise it. This was reflected in decreasing reaction times. Moreover, the strength of an action's trace correlated with activation in the bilateral pMTG, fusiform gyrus, as well as the mIPS. Activation of these areas was higher the weaker the trace was, quantified as negative logarithm of the trace strength. These areas are engaged in the processing of objects as well as associated manipulations (Schubotz et al., 2014), and form a functional hierarchy in action recognition (Kilner, 2011). The fusiform gyrus is the hierarchically lowest area in the revealed processing cascade: it has been reported to show a functional preference for processing manipulable objects (Martin, 2007), limited to their visual and tactile properties, rather than associated manipulations (Schubotz et al., 2014) or conceptual knowledge of the object (Peelen & Caramazza, 2012). Visual information about an observed object is fed forward from the fusiform gyrus to the pMTG as next higher area in the processing cascade. The pMTG has as well been associated with tool processing, but shows greater sensitivity towards object motion during their usage (Beauchamp & Martin, 2007) than towards their visual or tactile attributes. In a closely related vein, reaching for an object is processed in the mIPS (Vesia & Crawford, 2012), where activation was also higher with weaker trace strength. Previous studies have shown that activation in the areas of IPS and pMTG attenuates with the repeated encounter of the same action (Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013), as well as when the action could be successfully predicted based on preceding actions (Wurm et al., 2014). Activation in the fusiform gyrus and pMTG attenuates with repetition of objects (Martin, 2007). This effect is modulated by the overall probability of an object repetition (Mayrhauser, Bergmann, Crone, & Kronbichler, 2014).

Note that we cannot disentangle whether the observed correlation of activation with an action's trace strength resulted from an ease of recognition due to repeated exposure, or whether it reflects the prediction of a repeated encounter of an action based on its occurrence in the recent past. Research on sequence processing using M/EEG revealed that the sequential expectation of a stimulus and its repetition have a distinguishable effect on the event-related potentials evoked by a stimulus (Dehaene et al., 2015; Todorovic & de Lange, 2012). This suggests that the here

observed decreased activation in areas associated with action- and object-processing with a higher trace strength might also be due to both mechanisms, that is, the expectation of the repetition of a recently observed action, as well as suppression of activation due to the past exposures to that action.

## Conclusion

Human observers in the present study did not show evidence of using an artificial event structure to improve predictions of upcoming action steps. This finding adds to the proposal that *bottlenecks*, i.e. distinct states that need to be passed in order to change events or contexts, are crucial to identify structures (Solway et al., 2014). Instead of exploiting the event structure or sequential probabilities among succeeding actions, participants appeared to base their expectations solely on the frequency of an action in the recent past, which can be considered a frugal mechanism in the present setting.

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# 4 Discussion

## 4.1 Summary of presented studies

In three separate fMRI studies, I examined humans' ability to spontaneously detect and use different kinds of statistical structure to improve their predictions of observed upcoming action steps. In the first study (*Dissociating dynamic probability and predictability in observed actions – an fMRI study*; predictability study, hereafter; Ahlheim, Stadler, & Schubotz, 2014), I manipulated two aspects of a statistical structure underlying consecutive action steps: 1) an action step's predictability, that is, to which extent an upcoming action step could be predicted based on a preceding action, and 2) an action step's probability after a preceding action. An action step's probability depends on the respective action alone, whereas an action step's predictability reflects the number of concurrently possible action steps and their probability distribution.

Functional as well as behavioral results showed that participants implicitly used statistical regularities to inform their predictions of upcoming action steps. An action step's predictability and its probability had differential effects on the action's neural processing. Low probability of action steps was associated with an increase in activation in the intraparietal sulcus. This reflects the adaptation of the previously built internal model of the predicted upcoming action step. Low predictability of action steps enhanced activation in a fronto-parietal network, indicating that human observers integrated more information derived from an observed action step if predictability of the observed action step was low. The results from the predictability study were the first to show that humans are sensitive towards fluctuations in predictability and probability within a sequence of observed action steps and account for low predictability of upcoming action steps by exploiting more information provided by the action step.

This finding gave rise to the second fMRI study (*Prefrontal cortex activation reflects efficient exploitation of higher-order statistical structure*; higher-order study, hereafter; Ahlheim, Schiffer, & Schubotz, 2015). The higher-order study tested whether exploitation of statistical structure follows an efficiency criterion. I hypothesized that humans exploit information from more than one preceding action especially when the immediately preceding action is insufficient to predict the next action. To that end, I manipulated how much information a directly preceding action step (i.e. the 1st-order structure) provided on an upcoming action step. The more information was provided by the 1st-order structure, the more was predictability of an upcoming action step improved. I further manipulated how predictability changed under additional consideration of the penultimate action step (i.e., the 2nd-order structure). The independent manipulation of amount of information provided by the 1st- and 2nd-order structure allowed investigating how predictability based on the 1st-order structure influences humans' exploitation of information derived from the 2nd-order structure.

The results showed that human observers spontaneously took both 1st- and 2nd-order information into account to predict upcoming action steps. As hypothesized, 2nd-order information was exploited more when predictability based on the 1st-order structure was low. This indicates that humans exploit statistical information in a cost-benefit sensitive manner. As hypothesized, the rostrolateral prefrontal cortex (BA 10) balanced exploitation of statistical information. These findings provide first evidence that human observers adaptively select which kind of information to use in order to predict an observed upcoming action.

The last experiment (*Humans do not show use of an artificial event structure to predict observed actions*; event study, hereafter; Ahlheim, Balaguer, & Schubotz, 2015) tested whether human observers use a complex event structure organizing successions of action steps to

predict upcoming actions. Alternatively, humans might only rely on preceding action steps, rendering predictions less accurate. I created a statistical structure that allowed grouping of action steps into *events*, based on the associations between the action steps. Within one event, pre-defined transitional probabilities between action steps were implemented. Sequences of actions belonging to one event were occasionally interrupted by event-unspecific action steps, so that information on the current event could not be derived from preceding action steps alone. Surprisingly, neither behavioral nor fMRI data provided evidence for participants' use of the event structure. Instead, only an effect of recency information, that is, how often an action was seen in the recent past, was revealed *post hoc*. Possible reasons for this are discussed below.

## 4.2 Engagement of the AON by 1st- and 2nd-order structure

In all three studies, we found modulation of activation in the so-called action observation network (AON), which is composed of posterior temporal, inferior parietal and corresponding premotor sites (Caspers, Zilles, Laird, & Eickhoff, 2010). The AON shows increased activation when an action is observed irrespective of whether the observer is required to react towards the observed action (Caspers et al., 2010; Jeannerod, 2001). The predictability study found higher activation in the AON if an upcoming action step was less predictable. This points towards the network's sensitivity to fluctuations in predictability, or uncertainty, across a stream of observed actions. The higher-order study replicated this finding. Activation in the AON decreased more strongly if more information (formalized as a reduction of uncertainty) about an upcoming action step was provided by a preceding action step. Notably, in both studies, participants were neither told that action steps followed certain regularities nor were they instructed to predict upcoming action steps. The revealed modulation of activation in the AON by an action step's

predictability supports the idea that observed actions automatically trigger predictions of an action's further course (Hrkać, Wurm, & Schubotz, 2014; Kilner, 2011; Schiffer et al., 2013; Schubotz & von Cramon, 2008; Sebanz & Knoblich, 2009; W. Stadler et al., 2011).

Interestingly, improved predictability based on 2nd-order regularities showed differential effects on different parts of the AON in the higher-order study. Activation in the intraparietal sulcus (IPS) was decreased by improved predictability based on 2nd-order regularities. This shows that the IPS was similarly modulated by 1st- and 2nd-order information. The attenuation was revealed in the middle intraparietal sulcus (mIPS), which has a central role in execution as well as observation of reaching movements (Vingerhoets, 2014). The attenuation of activation in the mIPS reflects reduced processing costs of the observed action step, especially the reaching component of the action step, under improved predictability.

In contrast to the attenuation of activation in the mIPS, improved predictability due to 2nd-order information enhanced activation in the posterior middle temporal gyrus (pMTG). The pMTG is involved in processing tools and their associated motions (Beauchamp & Martin, 2007). Increased activation of the pMTG with higher 2nd-order predictability seems to contradict predictions made within the framework of predictive coding (cf. section 1.2.1). The most commonly reported finding for valid predictions is that of expectation suppression, that is, a reduced neural response for expected compared to unexpected stimuli (Summerfield & de Lange, 2014; Summerfield & Egner, 2009). Yet, a number of studies report the opposite effect, that is, a repetition or expectation *enhancement* of activation (Segaert, Weber, de Lange, Petersson, & Hagoort, 2013). Expectation enhancement possibly reflects the signature of a prediction, which is reflected in increased activation among a sub-population of neurons (Friston, 2010). Related to this is the notion of *perceptual sets*: it has been shown that during A/~A decisions, activation increases in areas

that code for the respective stimulus. The increased activation is interpreted as reflecting a perceptual template, or prediction, against which an incoming stimulus is matched (Summerfield & Koechlin, 2008b; Summerfield et al., 2006). Against this backdrop, the enhanced activity in the pMTG with higher 2nd-order information in the higher-order study can be interpreted to reflect the signature of the prediction of an upcoming object manipulation against which the observed action step is compared.

It is unclear why this increase of activation in the pMTG was solely found for improved predictability due to the 2nd-order structure. The pMTG showed reduced activation with higher predictability in the predictability study and for 1st-order predictability in the higher-order study. It can only be speculated that this was due to methodological differences. In the higher-order study, 2nd-order predictability showed a larger range, whereas variations of 1st-order predictability in the higher-order and the predictability study were smaller. Possibly, the combination of this larger range with the simultaneous modeling of 1st- and 2nd-order information allowed distinguishing effects of predictability in the pMTG. Further studies are necessary to test this interpretation and investigate more closely how a wider range of predictability of upcoming actions is reflected neurally.

Together, the results from the predictability study and the higher-order study show that human observers spontaneously exploit statistical information among action steps and provide strong support for the proposed role of statistical learning in action observation (Baldwin et al., 2008; Baldwin & Baird, 2001; Paulus et al., 2011; Zacks et al., 2007).

## 4.3 Possible explanation for differences in results

Surprisingly, neither a functional nor a behavioral effect of the event structure or the 1st- or 2nd-order probabilities was revealed in the event study. This stands in contrast to

the findings from the predictability and the higher-order study, as well as to other studies revealing learning of event structures among actions (Avrahami & Kareev, 1994; Baldwin et al., 2008) or abstract stimuli (Schapiro et al., 2013).

In order to investigate spontaneous use of event structure in sequences of action steps, it was necessary to modify the employed stimulus material and the cover task in the event study. In the first two experiments, participants watched videos showing continuous sequences of action steps that built upon each other. Although the construction within one video was not goal-directed (that is, no meaningful construction was achieved), the construct expanded with each action step. It was not possible to implement similar videos in the event study because the end of a video showing one action sequence would have likely dominated event perception. This would have prevented formation of events based on statistical regularities. To account for this, separate video clips for each action step were presented that did not build up on each other (cf. Baldwin et al., 2008, for a similar approach). Possibly, this discouraged participants' binding of action steps across different videos and impeded learning of transitional probabilities between action steps.

Moreover, the cover task implemented in the first two studies required participants to memorize which action steps had occurred within an action sequence (i.e., one video). Possibly, this facilitated detection of sequential regularities. In contrast, an object classification task (color: reddish or bluish) was implemented in the event study in order to obtain a behavioral measure during to the functional session. The rationale behind this task was that participants would benefit from detecting sequential regularities between actions. Participants' learning of the event structure was expected to result in quicker reaction times. Due to the nature of the video material, it is possible that participants relied on cues inherent to the evolving action to prepare their responses, for example, the actor's reaching direction. Thus, the task possibly drew participants' attention more strongly to perceptual

attributes of the current video. This might have hindered detection of sequential regularities between action steps in the event study. Support for this assumption comes from findings showing more robust statistical learning if attention is directed towards predictive stimulus dimensions (Jiang & Chun, 2001).

Additionally to the described changes of the experimental protocol, specific features of the statistical structure in the event study might also have prevented use of the transitional probabilities. Two features of a statistical structure influence the structure's complexity: the number of elements and the number of valid transitions between those elements. The complexity of the statistical structure implemented in the event study exceeded the complexity of the structures guiding action sequences in the other two studies. In the predictability study, only six different actions were used and $1^{st}$-order probabilities covered a broad range (from .25 to 1.0). The statistical structure implemented in the higher-order study was optimized to investigate exploitation of $2^{nd}$-order statistical regularities: First, the number of $2^{nd}$-order transitions was limited to only a subset of all possible combinations (only 128 out of the theoretically possible 512 combinations of three action steps). Second, substantial differences between $2^{nd}$-order probabilities were created (ranging from 12.5 to 87.5). Contrary to that, $1^{st}$- and $2^{nd}$-order probabilities in the event study were considerably less informative which made their exploitation less beneficial for predictions.

Findings from the higher-order study suggest that humans exploit additional information in a cost-benefit sensitive manner. A similar cost-benefit trade-off might have impeded detection of the implemented event structure in the event study. Due to the event structure, action steps had a high rate of occurrence as long as one event was ongoing. With beginning of a new event, action steps that had not occurred for a longer period were observed again. This effect was quantified as an action's *trace strength*, which reflected the

frequency of an action step in the recent past. The trace strength was the only measure for which an effect on reaction times and the fMRI data was revealed, albeit *post hoc*. Findings suggest that participants considered an action's trace strength alone, rather than investing into more effortful cognitive operations necessary to use the event structure or transitional probabilities between action steps. Possibly, the costs associated with exploitation of the event structure or transitional probabilities outweighed the gain in predictability of an upcoming action step compared to using an action step's trace strength alone.

This interpretation is in line with the concept of bounded rationality (Gigerenzer & Goldstein, 1996), which describes heuristic decision-making, as well as with theories on acquisition of abstract knowledge (Tenenbaum et al., 2011), for instance during category learning (Love, Medin, & Gureckis, 2004). These theories advocate the idea that humans only exploit more complex models of the world if a simpler model is not sufficiently precise. Considering only an action's recency (or trace strength) was possibly a well-suited frugal mechanism under the particular constraints inherent to the event study, as using any further statistical information might not have sufficiently improved prediction of upcoming actions.

## 4.4 Action goals: a prerequisite for event perception?

The three experiments of this thesis tested for an influence of an action's statistical structure on action prediction. To that end, contributions of action knowledge, for instance provided through inference of action goals, were excluded. Previous studies have shown that event perception does not require the presence of overarching goals, but can occur solely based on statistical regularities between action steps (Avrahami & Kareev, 1994; Baldwin et al., 2008; Buchsbaum et al., 2014). However, participants in the event study did not show evidence of using the event structure.

One notable difference to these previous studies is that events in the event study were ambiguous, as each action step was part of two events. Additionally, events had neither distinctive beginnings nor end-states and could start and end with each of three respective action steps. Both aspects could potentially have rendered the use of the event structure more difficult. End-states of a semantically unrelated sequence of action steps, like in the study by Baldwin and colleagues (2008), could act as substitutes for action goals that signal the completion of an event and the beginning of a new one. The prevalence of end-states of an event in previous studies possibly fostered learning of the event structure (Avrahami & Kareev, 1994; Baldwin et al., 2008; Buchsbaum et al., 2014), whereas absence of end-states in the event study might have prevented use of the event structure.

Developmental studies highlight that goals, as signals of an action's success, are important to learn the action (Elsner, 2007). An overarching goal aids binding a sequence of action steps together in one event (Buchsbaum et al., 2014). This is supported by a recent finding showing that activation in the AON attenuates with encounters of goal-coherent action steps that constitute an event (Wurm et al., 2014). Importantly, action steps of one event were presented interleaved with actions belonging to other events in the study by Wurm and colleagues. It was therefore not possible for participants to predict *when* the next action step of an event would occur, but only *which* action step should occur, based on the inferred goal of the event. The finding by Wurm and colleagues provides evidence that human observers link actions that belong to the same event across interruptions of the event. This shows that human observers do not base their predictions only on directly preceding action steps but can take an overarching event into account.

Events in the study by Wurm and colleagues (2014) developed linearly towards a goal (i.e. no action was repeated within an event). In contrast, events in the event study were recursively organized. In the light of the findings by Wurm and colleagues, it can be

hypothesized that event information is only maintained over an interruption if an event develops linearly. However, it is unclear whether an inferred action goal is necessary as well, or whether an arbitrary end-state of an event is sufficient (cf. Baldwin et al., 2008). In order to test this, artificial action sequences could be generated that accumulate evidence in favor of one or another final action (i.e., end-state) during their course. This evidence accumulation could be occasionally disrupted by uninformative action steps. If participants were able to maintain accumulated information up to the interruption, their prediction of the final action of the action sequence after the interruption would be improved. In contrast, if accumulated information was not maintained during the interruption, the prediction of the final action would be impaired. By testing whether or not human observers maintain accumulated information for semantically unrelated actions, the proposed experiment would improve our understanding of how humans come to use event information to predict upcoming actions.

## 4.5 Domain generality of findings

Early accounts on action observation proposed that prediction of other's actions is accomplished through an internal emulation of the observed action (Grush, 2004; Jeannerod, 2001). It is now widely accepted that prediction is not limited to actions (Schubotz, 2007) but forms a core operative mechanism of the brain (Clark, 2013). In line with this, the predictability and the higher-order studies revealed that prediction of upcoming actions is not accomplished by the AON alone but is supported by domain-general regions.

Additionally to higher activation in the AON, the predictability study revealed increased activation in a network composed of dorso-medial prefrontal cortex, the anterior insula, and the orbito-frontal cortex when predictability of an upcoming action was low.

This network is known to process uncertainty about a probabilistic outcome (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel, Song, & McCarthy, 2005; Mushtaq, Bland, & Schaefer, 2011; Volz, Schubotz, & von Cramon, 2005) and uncertainty during perceptual decision-making (Grinband, Hirsch, & Ferrera, 2006; Summerfield, Behrens, & Koechlin, 2011). This finding shows that action prediction is supported by domain-general areas outside of the AON.

This interpretation is further corroborated by the results of the higher-order study. It was found that the lateral BA 10 orchestrates efficient exploitation of 2$^{nd}$-order information. Previous research on the functional profile of the lateral BA 10 has focused on higher cognitive operations in abstract domains and hypothesized that the BA 10 contributes to the integration of sources of information (Badre, Doll, Long, & Frank, 2012; Ramnani & Owen, 2004, but see Golde, Cramon, & Schubotz, 2010). The engagement of the BA 10 during action observation seems to be inconsistent with these previous findings but supports the idea that processing in the BA 10 is domain-general.

Together, the results from the predictability and the higher-order study show that in dependence of different aspects of a statistical structure, different domain-general areas contribute to the prediction of upcoming action steps.

Different studies support the assumption that areas outside of the AON are engaged during action observation in dependence of current task requirements. For instance, two recent studies showed that observed actions recruit the parahippocampal gyrus if an action's context adds importantly to the action's understanding (Wurm & Schubotz, 2012), or the fusiform face area if an actor's identity contributes to an observed action's prediction (Hrkać et al., 2014). The involvement of additional areas during action observation depends on the difficulty of action recognition (Lingnau & Petris, 2013). These findings show that action observation is not limited to the action observation network.

Areas that are traditionally assigned to the action observation network also contribute to prediction of abstract stimuli (Schubotz & von Cramon, 2004; Schubotz, 2007), indicating that the AON cannot be reduced to prediction of observed actions.

The repeated observation of an additional engagement of domain-general areas during action observation supports the conclusion that limiting action observation and prediction to the action observation network is potentially misleading. It seems that this network is preferably, though not exclusively, recruited by observed actions and is flexibly extended by other functional areas in dependence of current task requirements.

If observed actions and abstract stimuli engage the same network, it could be questioned why basic cognitive mechanisms, such as efficient use of statistical information or detection of event structures, should be investigated in the framework of action observation rather than in abstract stimuli. As outlined in the introduction, actions are multi-dimensional stimuli: actions develop over time and challenge the observer with multiple possible sources of information on the temporal and spatial dimension. In order to successfully predict an observed action, relevant sources of information need to be identified. Thus, action observation provides an ecologically valid paradigm that allows us to investigate how the human brain can identify relevant sources of information and achieve successful prediction of observations in complex and multi-dimensional environments.

## 4.6 Generalizability to everyday actions

In the studies of this thesis, I used arbitrary, rather than everyday actions as stimulus material. I chose to do so because it is hard to quantify the underlying structure and statistical regularities in everyday actions. To what extent present results can be generalized to everyday actions might be debatable. One way to estimate predictability of

an upcoming action in everyday actions is by assessing the number of manipulations associated with the object involved in the action: the less manipulations are possible, the higher is the predictability of the action once the involved object is recognized. A higher number of possible object manipulations has been shown to result in increased activation in parts of the AON, that is, the IPS and the pMTG (Schubotz et al., 2014). This is in line with the results of the predictability study. Overlapping effects of predictability of an upcoming action in both artificial sequences of action steps and in everyday actions signifies that the findings of the predictability study can be generalized to everyday, non-arbitrary actions. It was moreover shown that activation in the AON attenuates with number of previous experiences of an action (Schiffer et al., 2013), which points towards an adaptation of the AON to current environmental regularities. In the light of these findings, I propose that the neural signatures of statistical information among actions can also be generalized to the processing of everyday actions.

It should be noted that a simplistic definition of *action* was used in the three experiments composing this thesis. As outlined in the introduction, descriptions of actions usually include a goal or intention level (Kilner, 2011). Goals describe the observable end-state accomplished by an action (often with a sequence of action steps; Csibra & Gergely, 2007); intentions refer to the mental state of the actor (that is, the overall "why" of the action; de Lange, Spronk, Willems, Toni, & Bekkering, 2008). Knowledge of an action goal allows for the retrieval of the most likely action steps that need to be executed to accomplish this goal (Csibra & Gergely, 2007; Wurm et al., 2014). If action goals are known, statistical regularities among action steps could be overridden. As an example, if a person knows that someone wants to perform a physics experiment, she would not be surprised to observe the person putting nails in two lemons instead of cutting them in half. Inferred action goals can be considered as further conditionals of the statistical regularities

between action steps. Still, it is necessary to keep the goal information constant in order to investigate the influence of a statistical structure among action steps alone on action processing. This motivated the decision to create artificial action sequences devoid of any overarching goal information in the experiments of this thesis.

A possible limitation of the presented findings is that action steps in all three studies were defined as compositions of one object and one object-specific manipulation. This poses an over-simplification from everyday actions where most objects can be manipulated in different ways. Which manipulation is observed determines which action should be expected next (for instance, an orange that was cut will be most likely squeezed next, whereas an orange that was peeled will be eaten). Thus, statistical regularities in everyday actions need to be learnt for the combination of an object and its manipulation. In contrast, the statistical structures in the present studies could have been learnt based on transitional probabilities between objects alone, without attending to their manipulations. Although this possibility cannot be excluded with certainty, it can be considered as unlikely for two reasons. First, objects inevitably trigger retrieval of their associated manipulations (Bach et al., 2014). This was shown in studies investigating object processing using TMS (Cardellicchio et al., 2011), or fMRI (Schubotz et al., 2014). Given the strong association between objects and their manipulations, it seems unlikely that object manipulations were not attended to and learnt as well in the present studies. Second, the effects of a statistical structure on action prediction were not limited to areas known to be sensitive towards object properties, as for instance the fusiform gyrus (Martin, 2007). The effects also encompassed areas like the IPS, which has been assigned a critical role in processing of reaching movements and manipulations (Grefkes & Fink, 2005; Hamilton & Grafton, 2006). Yet, in order to understand better which information within an action is preferably

exploited when detecting statistical regularities, it needs further studies that separately manipulate statistical regularities among manipulations, objects, and their compound.

## 4.7 Prospective study: temporal aspects of action prediction

Findings from the predictability study indicate that an action's predictability and its probability have distinct effects on an action's neural processing. Predictability and probability can be dissociated in time and should affect different points of an observed action: predictability influences processing of an action already before the action is recognized, whereas the action's probability can only elicit an effect at the moment of recognition. Due to the low temporal resolution of fMRI, findings from the predictability study cannot answer how an action's predictability and probability interact over time. Therefore, I propose to use electroencephalography (EEG) to investigate this question further. EEG is a well-established method to investigate processing of statistically structured sequences (Daltrozzo & Conway, 2014), which is reflected in distinct event-related potentials (ERPs) and oscillation activity. Candidate ERPs to reflect an observed action's probability are the P300 and the N400. Previous studies have shown that the P300 component in central-parietal regions is sensitive towards stimulus probability and attentional reorienting (Polich, 2007). The P300 is typically revealed in paradigms employing simple statistical contingencies. More complex statistical structures, as in artificial grammar learning, elicit components such as the N400 (Kutas & Federmeier, 2011). The N400 component has previously been explored in action perception studies (Kutas & Federmeier, 2011; Reid & Striano, 2008). Adults and young infants exhibit an N400 response to action sequences with surprising outcomes (Amoruso et al., 2013), or to implausible actions (Proverbio & Riva, 2009). Findings from language studies show that the N400 amplitude is not modulated by an event's predictability, but only by its

probability (Kutas & Federmeier, 2011). This suggests that it should also most likely only reflect an action's probability rather than its predictability.

Predictive processing of sensory events is furthermore linked to specific changes in neural oscillations. Unexpected stimuli have been found to cause an increase in gamma band activity, leading to the proposal that prediction errors are fed forward via gamma band activity (Arnal & Giraud, 2012). Accordingly, observation of actions with a low probability should result in higher gamma band activity. A prediction error is supposedly weighted by the precision (or uncertainty) of its prediction (Clark, 2013). A prediction's precision depends on the event's predictability. Thus, less gamma band activity should be observed for actions occurring with both low probability and predictability compared to actions that had a high predictability but low probability.

Anticipation of upcoming events has been associated with an increase in beta frequency (Arnal & Giraud, 2012), signaling the backwards propagation of the prediction. Beta band activity is thus a likely candidate to show sensitivity to the degree of predictability of an upcoming action.

To investigate which ERPs and oscillation frequencies are modulated by an action step's predictability and probability, the experimental paradigm implemented in the predictability study could be adapted to EEG requirements. A combination of videos of the action steps and still frames extracted from the videos could be used to measure ERPs and oscillations during passive observation of the action sequences.

# 5 Conclusion

Successful prediction of others' actions is a prime example of fascinating human cognitive abilities. Previous research has shown that different aspects of human action knowledge contribute to prediction of observed actions but did not address how knowledge about actions is acquired in the first place. The studies composing the present thesis demonstrate that predictions of observed actions can be based on statistical regularities among action steps. Human observers showed sensitivity towards predictability and probability of observed action steps. Observers furthermore accounted for low predictability by efficiently exploiting information provided by a higher-order statistical structure, a process mediated by the rostrolateral prefrontal cortex. However, when presented with action steps that could be grouped into events based on associations between them, participants did not show use of the emerging event structure. Instead, they seemed to rely on an action step's frequency of occurrence in the recent past, which was a potentially frugal mechanism in the present task. Together, the results of these studies point towards humans' capacity to make use of different statistical regularities in their environment. The revealed human sensitivity towards statistical structure in actions highlights the role of statistical learning in the development of our action knowledge.

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# 7 Abbreviations

| | |
|---|---|
| AON | action observation network |
| BA | Brodmann area |
| BOLD | blood-oxygen-level dependent |
| EEG | electroencephalography |
| ERP | event related potential |
| fMRI | functional magnetic resonance imaging |
| (m)IPS | (middle) intraparietal sulcus |
| MEG | magnetoencephalography |
| pMTG | posterior middle temporal gyrus |
| SRTT | serial reaction time task |
| TMS | transcranial magnetic stimulation |
| ToM | theory of mind |

# Curriculum Vitae

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Declaration by Doctoral Candidate
of Own Contribution to Presented Academic Manuscripts
with Two or More Authors
(Cumulative Dissertation)

Name of Doctoral Candidate: Christiane Ahlheim

Title of Dissertation: Neural Signatures of Statistical Structure in Observed Actions

**Academic Manuscript 1**

| | | | |
|---|---|---|---|
| Title | Dissociating dynamic probability and predictability in observed actions – an fMRI study | | |
| Author(s) | Christiane Ahlheim, Waltraud Stadler, Ricarda I. Schubotz | | |
| Journal | Frontiers in Human Neuroscience | | |
| Publication status: | not yet submitted | | |
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| | in review | | |
| | in revision | | |
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| | published | X | Year of publication: 2014 |

Description of your own contribution, **when authorship is joint**:

- mainly responsible for the study's conception and design*
- data collection*
- mainly responsible for analysis and interpretation of the data
- mainly responsible for drafting and revising of the article
- marked as corresponding author

* study design and data collection were carried out in the context of my diploma thesis; data were re-analyzed, interpreted and the manuscript drafted in the context of my PhD studies.

**Academic Manuscript 2**

| | | | |
|---|---|---|---|
| Title | Prefrontal cortex activation reflects efficient exploitation of higher-order statistical structure | | |
| Author(s) | Christiane Ahlheim, Anne-Marike Schiffer, Ricarda I. Schubotz | | |
| Journal | Journal of Cognitive Neuroscience | | |
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**Academic Manuscript 3**

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