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Research report

Reliability of sensory predictions determines the experience of self-agency

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ABSTRACT

This study examines the neurocognitive mechanisms underlying the sense of agency, that is, the experience of causing and controlling events in our environment. Specifically, we tested the hypothesis that the sense of agency depends on an optimal integration of different anticipatory signals, generated by motor and nonmotor systems. An established marker of pre-reflective agency experience is the suppression of cortical responses to actively generated feedback as compared to passively observed feedback, which was measured here by event-related potentials (ERPs). Sensory expectations based on motor-related and unrelated signals were induced by varying the probabilistic contingency between action and feedback, and by priming the feedback prior to the action. Moreover, simultaneous conscious agency judgments were assessed. A reduction of visual N1 response was found to self- as compared to externally generated feedback. In addition, the N1 was modulated by accurate anticipations based on prime stimuli, independent of the precision of motor predictions. Conscious agency judgments, in contrast, were enhanced by prime stimuli only in situations where no precise motor predictions of the action feedback were available. These results indicate that anticipatory signals arising from motor and nonmotor systems are integrated differently depending on the level of agency processing. Our findings suggest that, at a pre-reflective level, the brain's agency system relies on both embodied signals and nonmotor sensory expectations. At higher cognitive levels, motor and nonmotor cues are weighted differently depending on their relative reliability in a given context, thereby providing a basis for robust agentive self-awareness.

1. Introduction

The experience of being the cause of one's actions and controlling sensory events in the environment serves as a key motivational force for human behavior. The term agency refers to the capacity for instrumental action, which is based upon the ability to perceive dependencies between actions and their consequences. An important source of signals contributing to this form of self-awareness is foreknowledge or predictive processing of the sensory consequence that follows an action [1–3]. Pathological disruption of the sense of agency has been associated with deficits in internal prediction mechanisms, for example, in the case of schizophrenic patients with delusions of control, i.e., misattribution of actions to external causes [4].

Internal sensory predictions, that is, internal models of future bodily states or environmental events following an action, can be generated by the motor system [5]. In addition, sensory predictions can also arise from various other systems, which take the current context, previous perceptual experiences and other predictive cues into account [[6] for review, see Ref. [7]]. Research on the neurocognitive basis of the sense of agency has focused mainly on sensory predictions of the motor system. Several studies have demonstrated that explicit agency judgments strongly depend on the comparison between a sensory expectation derived from efferent information and the actual sensory feedback following the self-generated movement [8–10]. It has been suggested that the experience of agency for the sensory event emerges in cases where the action outcome matches the initial expectation. Another line of research, in contrast, ascribes a crucial role to expectations arising independent of the operation of the motor system [11,12]. For example, it has been shown that inducing a representation of the sensory consequence prior to the action by means of priming enhances the conscious experience of agency [13], even if efferent signals are absent [2]. Furthermore, this effect is present for supraliminal as well as subliminal primes, that is, no matter whether the prime stimulus is conscious or not [14,15].

These proposed agency cues arising from different systems are not mutually exclusive, however. A current theoretical framework suggests that the brain's agency system combines and integrates different cues depending on their relative reliabilities in certain contexts and depending on the level of agency registration [16,17]. The present study aimed to test this hypothesis of optimal cue

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integration by comparing the impact of different types of sensory predictions at two levels of agency registration, at the implicit, sensorimotor level, and the explicit, higher-order cognitive judgment level. It is important to note that most studies exclusively focus on higher cognitive levels of agency processing by measuring explicit judgments of agency only. This, however, does not do justice to the complex phenomenology of agency and to the fact that in our everyday lives, a non-reflective experience is more common than an explicit representation of selfhood. At least two different levels of agency representation can be distinguished, a reflective and a pre-reflective level, and it has been proposed that different cognitive cues are combined to establish one or the other representation [16]. A measure that has been used to quantify the pre-reflective level of agency is self-specific sensory suppression, which refers to the fact that the sensory intensity of self-generated events is lower than for external events [16,18,19].

Sensory suppression is reflected for instance in the phenomenon that you cannot tickle yourself since self-produced tactile sensations are perceived as less intense as compared to the same sensations produced externally [20–23]. Neuroimaging studies have found suppressed neural activity in sensory areas specifically in response to self-generated sensory input [24–26]. Moreover, the N1 component of the event-related potential (ERP) has been proven to reflect an early indicator of this self-specific sensory gating. In fact, there are a number of studies showing a reduction in N1 amplitude when a sound is self-generated as compared to when it is externally generated [26–29]. Similarly, the visual N1 has also been found to be sensitive to the distinction between self-causality vs. external causality [30,31].

The explanation of sensory suppression is based on the idea of forward models of motor control generating predictions of the sensory consequences of a motor command, which are compared to the actual sensory feedback and removed in case of a match [20,32]. This predictive mechanism serves to signal unexpected changes in the environment. It can further be used to distinguish self- from externally generated sensations, and therefore serves as an indicator of the sense of agency, in particular, at the pre-reflective level of agency. However, the precise nature of the predictions used to gate afferent sensory information with regard to the spatial, temporal and qualitative characteristics of the sensory event are still not clear [33].

The present study investigated how sensory predictions from different cognitive systems are integrated by the agency system depending on the specificity and reliability of each source of information. To this end, the contingency between a specific type of action and a specific type of visual consequence was varied between high (75%) or low (50%) so as to create contexts in which highly specific and precise motor-related predictions were available or not. Furthermore, sensory expectations independent of the motor system were induced by priming the visual action consequence prior to the action. The EEG was recorded while participants self-generated visual stimuli by key press. We measured the amplitudes of the N1 component of the visual ERP to those stimuli to examine pre-reflective agency registration and, moreover, participants' explicit perception (i.e., judgments) of causality was obtained to examine the reflective level of agency experience. In a second task, which served as a control, subjects passively observed the same visual stimuli and it was tested whether sensory predictions can have a similar effect on both the N1 component and on causality judgments independent of the execution of an action.

According to the hypothesis of optimal cue integration [16], the agency system should apply higher weight to the more reliable information sources. Therefore, we predicted that prime-induced expectation of the action consequence should enhance the sense of agency more strongly (i.e., as reflected in a reduction of N1 amplitudes to self-generated effects and an enhancement of agency judgments) if no precise motor-related predictions are available. The specificity of these influences for agency processing was examined in direct comparison with effects during passive observation. Furthermore, the nature of motor predictions underlying sensory suppression, that is, the precision, timescales and types of those predictions, is still under debate. While some studies have demonstrated that temporal proximity [20,21] and precise spatial predictions [20] are important, others suggest that the mere presence of embodied (i.e., motor-related) signals is sufficient, and proximity of the sensory event or precision of sensory predictions does not matter [33,34]. Hence, if sensory suppression indeed depends on the precision of forward models of the motor system, we should observe a reduction of N1 amplitude in conditions of high as compared to low action–effect contingency.

2. Methods and materials

2.1. Subjects

Twenty-three healthy right-handed adults (20–32 years old, mean age 24 years, 11 female), with normal or corrected-to-normal vision participated in the after providing written informed consent, and in accordance with the Declaration of Helsinki.

2.2. Agency paradigm

A combination of an agency judgment paradigm [14] and a sensory suppression paradigm [29] was used. The experiment consisted of three different tasks: the motor–effect (ME), the effect-only (E) and the motor-only (M) task (see Fig. 1). In the ME task, a visual stimulus was generated by the participant's action, whereas in the E task, the visual stimulus was externally generated and passively observed. The E task was included to replicate self-specific sensory suppression as reported by prior studies comparing ERPs during observation of sensory events linked to an action and passive observation hereof, as well as to test whether experimental effects are specific for processing sensory effects as action feedback (i.e., agency effect). The M task, in which the participant's action did not produce a visual stimulus, served as a control to rule out motor activity as a possible confounding factor in the comparison between the ME and E task.

In the ME task, participants responded to a target stimulus (circle or square, presented for 50 ms) with a left or right key press according to a fixed stimulus–response mapping (counterbalanced across participants) without speed instruction. The key press triggered a visual effect stimulus (with a delay of 20 ms), which consisted of a set of three arrows (500 ms) pointing either upwards or downwards. Visual stimuli were presented in black on a gray background subtending a visual angle of $0.5^{\circ} \times 2^{\circ}$. For each block of trials, participants were asked to observe and judge the relation between their action (left or right key press) and the type of effect stimulus (up or downward direction of the subsequent arrows).

Two experimental factors were manipulated: action–effect contingency and prime–effect congruency. First, the contingency between action and effect (i.e., the predictability of the type of effect stimulus on the basis of the action) could be either high (75%) or low (50%). For example, in the high contingency condition, 75% of the up arrows were related to the left key and 25% to the right key (and vice versa for down arrows), whereas in the low contingency condition, up and down arrows were associated equally (50%) with both left and right key. This target–effect mapping was counterbalanced across participants. Second, priming was used in order to induce sensory anticipations prior to the action. Each trial started with the presentation of a mask stimulus (150 ms, composed of up and down arrows superimposed on each other) followed by the prime (40 ms) and another mask stimulus (20 ms). The prime stimulus was either identical to the future action effect (congruent priming) or consisted of arrows pointing in the opposite direction as the effect stimulus (incongruent priming). The interstimulus interval between action effect and forward mask was randomized between 1200 and 1800 ms.

To be consistent with previous studies, both experimental factors, priming and contingency, were manipulated between blocks [14,18]. That is, for 40 successive trials (i.e., one block), participants experienced constant levels of reliability of only one, both or none of the available cues. We sought to investigate how the relative reliability of a particular cue determines the subjects' implicit strategy of recruiting this cue as an agency indicator. Participants performed three blocks for each condition (high contingency: congruent and incongruent priming; low contingency: congruent and incongruent priming). After each block, participants judged the causal relation between their action (left/right key press) and the subsequent effect (up/down arrow) on a visual analog scale (VAS) ranging from 0 (no relation) to 100 (perfect relation). In total, participants performed 12 blocks of the ME task.

In the E task, participants passively watched the same visual stimuli used in the ME task, that is, without the instruction to press a key. The former effect stimuli were now externally generated by the computer with identical inter-stimulus timing as in the ME task. The factors contingency and priming were also varied in blocks of 40 trials, with a total of 12 blocks, as in the ME task. For each block, participants were