

# Extending experiences of voluntary action by association

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Edited by Walter Sinnott-Armstrong, Duke University, Durham, NC, and accepted by Editorial Board Member Michael S. Gazzaniga June 13, 2016 (received for review November 11, 2015)

**“Sense of agency” refers to the experience that links one’s voluntary actions to their external outcomes. It remains unclear whether this ubiquitous experience is hardwired, arising from specific signals within the brain’s motor systems, or rather depends on associative learning, through repeated cooccurrence of voluntary movements and their outcomes. To distinguish these two models, we asked participants to trigger a tone by a voluntary keypress action. The voluntary action was always associated with an involuntary movement of the other hand. We then tested whether the combination of the involuntary movement and tone alone might now suffice to produce a sense of agency, even when the voluntary action was omitted. Sense of agency was measured using an implicit marker based on time perception, namely a shift in the perceived time of the outcome toward the action that caused it. Across two experiments, repeatedly pairing an involuntary movement with a voluntary action induced key temporal features of agency, with the outcome now perceived as shifted toward the involuntary movement. This shift required involuntary movements to have been previously associated with voluntary actions. We show that some key aspects of agency may be transferred from voluntary actions to involuntary movements. An internal volitional signal is required for the primary acquisition of agency but, with repeated association, the involuntary movement in itself comes to produce some key temporal features of agency over the subsequent outcome. This finding may explain how humans can develop an enduring sense of agency in nonnatural cases, like brain-machine interfaces.**

volition | sense of agency | involuntary movement | intentional binding | transcranial magnetic stimulation

In a series of brilliant experiments, Roger Sperry switched the nerves for flexion of the rat hind leg with the nerves for extension. After that, whenever the bottom of the foot was injured, the rat extended the foot instead of flexing it. Rats never learned to lift up the paw, and “no adaptive functioning of the nervous system took place” (1). When the optic nerves of salamanders were cut, and the eyeball rotated 180°, salamanders saw upside down for the rest of their lives (2). These experiments suggested that key sensorimotor brain circuits are largely hardwired, and impervious to modification by experience.

“Sense of agency” refers to the capacity to control one’s actions and, through them, the external world. Sense of agency is fundamental to instrumental and goal-directed actions, and forms the cornerstone of humans’ astonishing capacity to change their physical and social environment (3). However, it remains unclear how the brain produces this distinctive and important subjective experience. Some recent results have linked the sense of agency to specific preparatory volitional signals in frontal (4) and parietal (5) areas, which then trigger voluntary motor commands passing through the “final common path” (6) of the primary motor cortex. Importantly, these “volitional signals” were generated well before the occurrence of both action and outcome, and were strongly correlated with the subjective intention to move. Such theories suggest a hardwired, Sperryesque account of human volition.

In contrast, associative theories of agency deny the special status of internal volitional signals and focus instead on cooccurrence of

actions and outcomes. For example, in ideomotor theories, repeated association of actions and outcomes means that, over time, actions come to be represented primarily in terms of their anticipated outcomes or goal-states. By the same association, activation of the neural code for the goal event is then able to generate the voluntary action (7). Stronger versions of this view suggest that people merely infer their own agency based on observing the combination of action and outcome. There is no direct mental access to the internal processes that cause our actions, and the experiences of will and agency are mere inferences or even illusions (8).

Current computational models of motor control, such as the comparator model (9, 10), have also been used to explain sense of agency. During action execution, efferent signals from motor areas are compared with predictions about the sensory consequences of the actions, such as feedback from a moving limb or from some other external outcome of the action; these signals and predictions contain elements of both the hardwired and the associative frameworks. On the one hand, the sense of agency could depend necessarily on hardwired efferent motor signals. On the other hand, the predictions generated by this signal must be based on learning an internal model from previous associations between efferent signals and their sensory consequences, consistent with the associative framework. It remains unclear to what extent human sense of agency is based on such hardwired signals or on learned associations.

These models make different predictions about the possibility of transferring agency from a voluntary action to another, cooccurring event. Mental properties commonly transfer from representation of one event to representations of another, notably in classic conditioning (11), but it remains unclear whether this occurs also for sense of agency. We asked participants to trigger a tone by making a

## Significance

**In everyday life, people feel in control of their voluntary actions and their outcomes. This “sense of agency” could reflect hardwired brain signals for volition, or could be acquired by repeated association between a goal-directed action and another event. By pairing voluntary actions of one hand with involuntary movements of the other hand, we showed that key aspects of agency experience can transfer from voluntary to involuntary movements. Our results explain why one can feel fully in control of one’s actions even when they are performed automatically, without focal conscious attention. We suggest that sense of agency depends on a metacognitive signal that is relatively nonspecific. Our findings could guide acquisition of voluntary control using neuroprosthetics and brain-machine interfaces.**

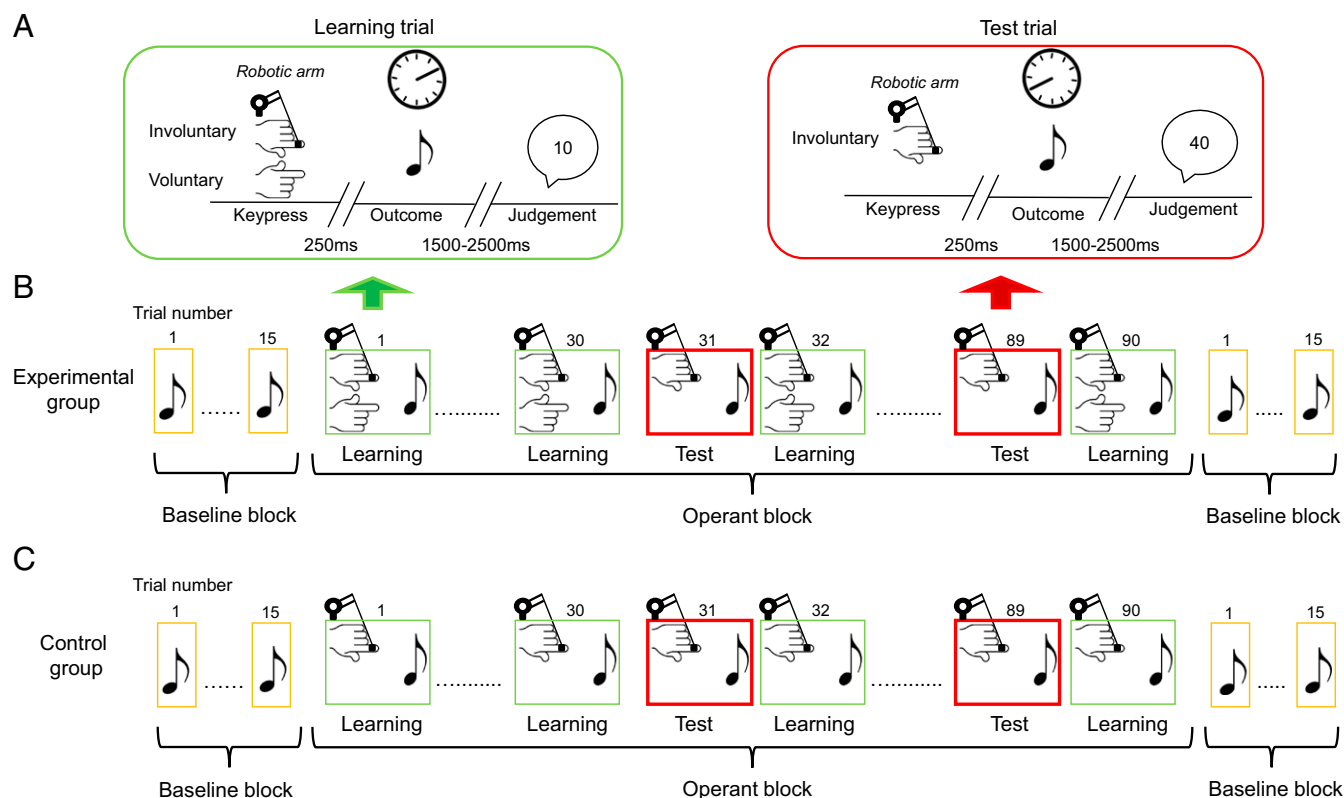
Author contributions: N.K. and P.H. designed research; N.K. performed research; N.K. and P.H. analyzed data; and N.K. and P.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. W.S.-A. is a Guest Editor invited by the Editorial Board.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1521223113/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1521223113/-DCSupplemental).



**Fig. 1.** (A) Timeline of an experimental trial. In the learning trials (Left green box), participants were instructed to press the enter key on a keyboard in front of them with their right index finger at a time of their own free choice. This action was paired with involuntary keypress (Left control key) induced by a robotic arm pressing on the left index finger. In operant blocks, each keypress was followed by a beep (1,000 Hz) after 250 ms. At the end of the trial, participants reported the perceived time of the beep. See *Materials and Methods* for full explanation. (B) In the experimental group, the session started with a baseline block. The operant block then ensued. Voluntary actions of one hand were paired with involuntary movements of the other hand, followed by a tone 250 ms. After an initial learning phase of 30 trials, further learning trials were interleaved with test trials (A, Right red box) on which involuntary movements were followed by tones, but no voluntary action occurred. The session ended with the execution of a further baseline block. (C) A group of control participants followed the exact same design as the experimental group, but their involuntary movements were never associated with voluntary actions. In both groups, data from the test trials (red bold boxes) was used for analysis. The corresponding trial number is shown above each box. For Exp. 2, robot-induced movements were replaced with TMS-induced twitches.

voluntary keypress action with one hand. The voluntary action was always associated with an involuntary movement of the other hand. We then tested whether the combination of involuntary movement and tone alone might suffice to produce a sense of agency over the tone, even when no voluntary action was now present. Theories based on hardwired efferent signals predict no sense of agency in this condition, because the putative internal volitional signal for one's own voluntary actions is, by definition, absent for involuntary movements. In contrast, associative learning theories predict that repeated cooccurrence of a voluntary and an involuntary movement could produce associative transfer, so that involuntary movements could, by association, come to acquire the same sense of agency that characterizes voluntary movements.

We therefore designed two between-subject experiments. Thirty-six participants were recruited for the first experiment and were randomly assigned to the experimental and control groups (Fig. 1). In the experimental group, self-paced voluntary keypress actions of the right hand triggered an immediate and physically similar involuntary keypress movement of the left hand, imposed by a robotic arm (Phantom Premium, 3D Systems). These movements were followed by a tone 250 ms later, in the operant condition. Participants could thus learn to associate voluntary action, involuntary movement, and tone. Such "learning" trials alternated with "test" trials containing only involuntary movements followed by tones, and no voluntary action. Sense of agency over the tone was measured using an implicit marker based on time perception. Participants judged the time of the tone using a

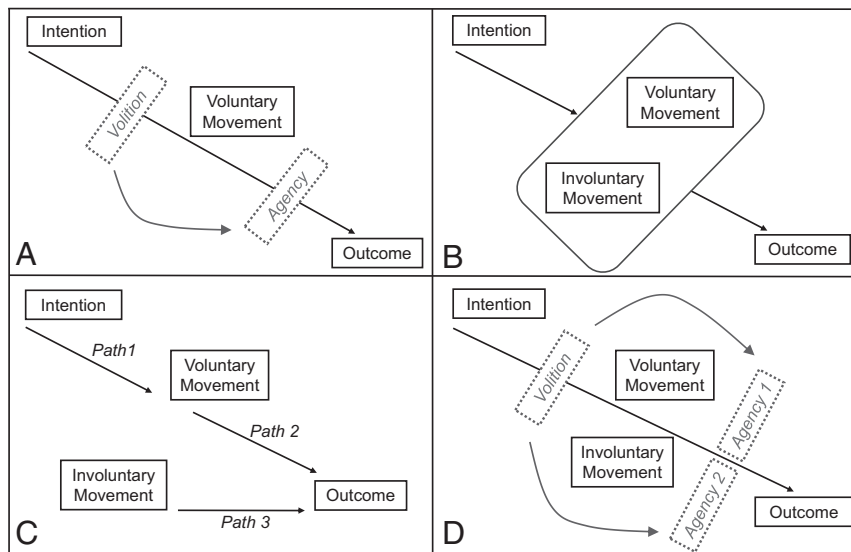
rotating clock display. A shift in the perceived time of the tone toward the preceding action is an established implicit marker of agency. This shift is compared with a baseline condition containing only a tone and no action. Importantly, involuntary movements are not sufficient to cause perceptual shifts of the tone, and a volitional signal appears necessary (12–14). A further control group of participants also judged the time of the tone following an involuntary movement, but had never experienced any association between involuntary and voluntary movement. Kinematics of both hands' movements were monitored online using accelerometers.

Exp. 2 used the same design but triggered involuntary movements by noninvasive brain stimulation. Thirty-six participants were recruited and were randomly assigned to experimental and control groups. Self-paced voluntary actions of one hand were now paired with involuntary twitches of the other hand, caused by transcranial magnetic stimulation (TMS) over the primary motor cortex. These learning trials again alternated with test trials containing only involuntary TMS-evoked twitches followed by tones. Motor-evoked potentials were recorded from the first dorsal interosseous of the left hand. The control group also judged the time of the tone following an involuntary twitch, but they had never experienced any association between the twitch and any voluntary actions.

If sense of agency depends on a hardwired efferent signal from the voluntary motor system, no amount of associative learning should be able to induce key temporal features of experience of agency for involuntary movements followed by tones, because







**Fig. 3.** A possible mechanism for agency transfer. (A) Voluntary actions are often associated with subjective experience of volition and agency. (B) In our experimental group, we rewired this association so that the participants' intention produces two movements, one voluntary and the other involuntary. (C) Pairing voluntary and involuntary movements lead to key temporal features of agency being experienced when involuntary movements were followed by outcomes (path 3). This experience, however, strongly depended on its previous association with intention which precedes the voluntary action (path 1). (D) This suggests that once a voluntary signal is present, it can be mentally associated with other events, and spread to drive key temporal features of agency with respect to other movements.

**A Path Model of Agency Acquisition.** In our everyday life we perceive our voluntary actions as caused by our intention to produce a specific outcome. These voluntary actions are often associated with two specific experiences: The experience of volition reflects the initiation and control of the voluntary action, and possibly a prediction of the outcome. In contrast, the experience of agency is based on attributing the actual outcome back to one's own triggering action (15) (Fig. 3A). In our experiment we reprogrammed the experiences surrounding voluntary action by making participants perform two movements at the same time: one voluntary and the other involuntary (during learning trials). Thus, the intention to initiate the voluntary action was associated with two movements, one located on each hand (Fig. 3B). Classic intentional binding predicts that experience of agency arises when there is both a direct relation between a movement and its outcome (path 2 in Fig. 3C), and also a direct relation between the movement and the intention which precedes it (path 1 in Fig. 3C). The necessity of path 1 is clear from previous results (12, 14), showing that intentional binding does not occur for involuntary movements.

In our experimental group, a further path (path 3 in Fig. 3C), similar to path 2, also exists between the involuntary movement and the outcome. Data from our experimental group shows that this path can generate some key temporal features of agency, such as intentional binding. Importantly, comparison with the control group shows that functioning of path 3 strongly depends on its previous association with internal volitional signals (path 1 in Fig. 3C). For the control group, the involuntary movement was never paired with the voluntary action, and involuntary movements never showed the key temporal linkage to outcomes. This finding suggests that a single volitional signal can drive multiple action–outcome relations. As a result, some key temporal features of agency can arise for movements that are merely correlated with an intention, but not directly caused by it. This finding, in turn, suggests that the relation between intention and sense of agency is not precisely matched, and is not effector-specific (Fig. 3D).

**Can We Be Mistaken Regarding the facts of Our Own Agency?** Explicit measures of agency are subject to a number of cognitive biases and are highly sensitive to task demands. We therefore advisedly chose

an implicit measure of sense of agency, based on time perception. Synofzik et al. (16) suggested that sense of agency comprises two different levels: an implicit “feeling of agency” and an explicit “judgement of agency.” Based on this view, the feeling of agency is produced implicitly by low-level sensorimotor signals. In the rare case that one must explicitly judge one's own agency, this low-level feeling of agency provides the primary evidence for the judgement. However, social contextual cues and other priors can bias such judgements. The intentional binding task focuses on the nonconceptual feeling of agency. We did not obtain explicit judgements of agency in this task. As a result, we cannot know whether the involuntary movements of the experimental group came to feel like “I did that,” but we imagine they did not.

In healthy adults, voluntary and involuntary movements generate quite different experiences (17), and our brief training was unlikely to suppress this difference. Indeed, most systems of law are based on a “voluntary action condition,” which rigidly assumes a distinct subjective experience of voluntary action (18). In particular, selection and preparation of action in frontal motor areas appears essential for a full experience of voluntary control (19). Nevertheless, our results show that some key features of sense of agency can be transferred from voluntary to involuntary movements, given appropriate associative learning. The experience of the tone following involuntary movement acquired some temporal features of agency, but this does not imply that participants would judge themselves the author of the tone. Here, we have used implicit measures to show that one key feature of voluntary action, namely the important “goal-directed” or “ideomotor” feature, by which the experience of action leads to anticipation of outcomes, can transfer to involuntary movements. Interestingly, patients with psychosis may have a deluded experience of their own actions, which frequently involve false-positives, such as reporting voluntary control over external events unrelated to their own actions, such as changing traffic lights or news events.

Our results can also be interpreted using an active inference framework (20). Here, intentions are abstract predictions about likely outcomes, which are Bayes-optimally combined with sensory evidence about outcomes when this becomes available. Intentional binding has been modeled as a Bayes-optimal integration of action and outcome (21). Thus, strong tone binding might arise because

intentional actions provide a high-precision prior for estimating outcomes. We found that pairing a second event—in this case an involuntary movement—with a high-precision intentional prior, results in that event having a similar influence on outcome perception to the original intentional action. Thus, the structuring effects of voluntary action on outcome perception may not reflect some unique experiential quality specific to volition (however, see ref. 22), but simply that intentional actions normally serve as high-precision priors for their outcomes.

#### **Specificity of Internal Volitional Signals Underlying Agency Acquisition.**

We conclude that an internal volitional signal is required for the acquisition of sense of agency. However, after repeated association, the volitional signal is not required for subsequent expression of key temporal features of agency, such as intentional binding. Moreover, the putative volitional signal is not highly specific with respect to which agency relations are established. In our case, volitional signals controlling the right hand lead to intentional binding for involuntary movements of the left hand. Thus, a range of movement/outcome pairings may be enabled by cooccurrence with intention. Intentions do structure subsequent subjective experience, but by means of a loose fit rather than a tight prediction about specific muscular movements. Previous studies suggested that the sense of agency is highly temporally specific, in that intentions, actions, and outcomes must follow a predictable temporal sequence (19, 23). However, the content of intention, action, and outcome can be combined arbitrarily without compromising the experience of agency. Our result suggests that volitional signals have the interesting property of high “latent associability”: they potentiate the development of any operant relation with which they cooccur. This finding is consistent with Skinner’s demonstration that animals assume a causal connection between an action and a reinforcing stimulus, even when the connection is in fact an accidental correlation (24).

In our case, the path between volition and agency is not effector-specific, but effector-independent. In particular, our design involved voluntary actions and involuntary movements assigned to different hands. Our results thus suggest that the contribution of internal volitional signals to sense of agency is bihemispheric, rather than hemisphere-specific. Rodent studies showed that mice readily learn to control a robot when arbitrary motor cortex activity is used to drive the robot dynamics. Learning such intentional neuroprosthetic skills depends on corticostriatal plasticity (25). Our results similarly show that linking formation of an intention to an outcome leads to formation of some key temporal features of agency, even when the means that mediate between intention and outcome are artificial, and even after the original volitional signal is dropped. These findings may explain how humans can develop an enduring and successful feeling of agency in cases of nonnatural movement, like brain–machine interfaces (26).

**Learning One’s Own Agency.** Our experiment suggests that a conjunction of three conditions may be sufficient for sense of agency. First, an internal volitional signal must be present to provide a general metacognitive experience of intentional action. Second, some body movement must occur. Third, some external outcome of the action must occur. We also showed that no specific linkage between the metacognitive volitional signal and the body movement is necessary. In particular, the volitional signal need not be present at the same time as the body movement, nor even relate to the same effector. Thus, the internal volitional signal need not have a hardwired connection to the motor output system in the manner suggested by Sperry. In our experiment, it was sufficient that the volitional signal and the body movement had previously been associated.

This pattern of results reflects two fundamental features of human voluntary action, which we call “automaticity” and “flexibility.” Automaticity refers to the way that actions that initially

require focused attention, such as driving a car or cooking soufflés, become increasingly fluent with repetition. The subjective experience of action also changes. The action becomes less central in conscious experience, and instead provides a background “buzz” of awareness (16). However, outcomes are still fully attributed to one’s own agency. Our results show a similar retention of key temporal features of experience of agency even when our experimental design deliberately reduced and removed intentional control over the outcome. Thus, our study can clarify a striking paradox of human action: namely, that one can feel fully in control of a skilled action, such as riding a bicycle, and have a clear sense of agency, yet have only thin conscious experience of the action itself.

Flexibility refers to the ability of humans and animals to achieve control over goal states using complex and varying means (27). This perhaps contributes to the astonishing human proficiency in developing and using technology. Hebb’s classic concept of motor equivalence (28) suggests that cognitive systems are not generally concerned whether a goal is achieved with one effector or with another; all movements that achieve the goal are effectively equivalent.

This transfer of key temporal features of experience of agency from intentional actions to other movements recalls the way that sense of agency emerges in human development. Human infants appear to act randomly, with little intentionality and goal-directedness, compared with healthy adults. During early experience, infants may gradually learn the precise mapping between different intentions, the resulting body movements, and external consequences. Infants thus eventually acquire the capacity to move a specific effector, achieving control over their body and thus over their environment. Our results show that the capacity to form new intention–movement–outcome associations seems to remain and, importantly, could be generalized to non-voluntary movements, even when intentional action is no longer present. In this regard, it has been shown that younger children tend to confuse intended with accidental outcomes (29–31).

Our experiments suggest that a hardwired internal volitional signal is required for the initial acquisition and emergence of sense agency. Importantly, this hardwired signal appears to be cognitive rather than motoric, because it is not linked to any specific output effector. At the same time, associative mechanisms contribute strongly to the expression of sense of agency. The presence of internal volitional signals during learning (path 1 in Fig. 3C) is necessary for induction, although not expression of key temporal features of experience for both direct voluntary action (path 2 in Fig. 3C), and also for an associated involuntary movements (path 3 in Fig. 3C).

Wittgenstein (17) famously asked, “What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?” Sense of agency is a partial answer to this question. However, even simple voluntary actions trigger widespread and automatic involuntary elements. For example, voluntarily lifting the right arm requires anticipatory compensations in contralateral muscles (32, 33). Thus, voluntarily moving one effector normally leads to involuntary (or at least less voluntary) adjustments elsewhere, as in our experimental group. Importantly, people are not generally surprised or even aware of these involuntary adjustments, although they would presumably be immediately conscious of a comparable passive displacement of the same body parts. Thus, the involuntary side-effects of voluntary action come to form part of an integrated experience of agency (16). The highly distributed, integrated nature of motor control ensures very frequent association between voluntary actions and involuntary movement. We suggest that this fact lies at the heart of our finding of extensible sense of agency.

In conclusion, we suggest that some key temporal aspects of experience of agency, namely the perceptual anticipation of an action outcome, can be transferred from voluntary actions to

involuntary movements. Such transfer follows repeated co-occurrence of an internal volitional signal, with both an involuntary body movement and a sensory outcome. Importantly, association with an internal volitional signal appears to be necessary to initially establish key temporal features of agency with respect to an involuntary movement, but is not necessary for its subsequent expression. The transfer process thus resembles the development of an enduring sense of agency that emerges during skill learning, as action control progresses from focused and effortful to automatic. Interestingly, the involuntary movement that becomes associated need not match the intention precisely, suggesting that the metacognitive signals supporting agency acquisition are relatively nonspecific. The high latent associability of these signals may reflect the distributed nature of motor control. Recent successes in acquisition of voluntary control using neuroprosthetics and brain-machine interfaces testify to the latent associability of human sense of agency.

## Materials and Methods

Upon arriving, participants read the information sheet and gave written informed consent. In Exp. 1, participants' left index finger was attached to the distal end of the robotic arm and was placed on the left control key. The right index finger was placed on the enter key. The intentional binding task was explained for the participants and they were familiarized with the robotic arm-induced passive movements. Two accelerometers were mounted on the left and right index fingers and participants were asked to wear headphones (Sennheiser). The experiment started with the baseline block (15 trials). In this block, participants were instructed to look at a rotating clock but not to press any key. In each trial, a tone was played and participants judged the clock hand position at the time of the tone. This block was followed by the operant block, where the tone was always caused by participants' keypress at a time of their own free choice, 250 ms later. Like the previous block, participants were asked to judge the clock hand position at the time of the tone. In the experimental group, in the first 30 trials of the operant block, voluntary keypresses of the right hand were paired with the involuntary keypresses of the left hand. These learning trials were followed

by 30 test trials, where a command appeared on the screen and instructed participants not to make any voluntary keypress with their right hand. Meanwhile, at a random time, participants made a passive keypress with their left hand. As in previous trials, participants made judgements about the time of the tone that followed their keypress. These test trials were interleaved with another 30 learning trials. Therefore, each operant block consisted of 60 learning trials and 30 test trials. In the control group, participants never made any voluntary action; therefore, their learning trials only consisted of passive keypress with the left hand. In both groups, the experiment finished by performing another baseline block.

Exp. 2 followed the same principles as in Exp. 1 with the following differences: participants were asked to place their left hand on the desk next to the keyboard. Robotic arm-induced movements of the left index finger were replaced with TMS-induced twitches. The TMS coil was optimally positioned in each subject to produce involuntary movement of left index finger, minimizing contraction of more proximal muscles and muscles activating other joints. The headphones were replaced with loudspeakers. Accelerometers were replaced with surface electrodes for electromyography. As in the previous experiment, participants made judgements about the time of the beep in three separate blocks.

Judgement error was calculated by measuring the difference between the judged clock time and the actual time. The averaged judgement error across the trials was then calculated for each block. "Tone binding" was defined as the difference between the judgement error in the operant and the baseline condition. The negative value of tone binding represents the perceptual shift of outcome toward its action. Tone binding data from the test trials only were used for analysis.

Experimental design and procedure were approved by the University College London Research Ethics Committee, and followed the principles of the Declaration of Helsinki. Transcranial magnetic stimulation followed established safety procedures (34).

**ACKNOWLEDGMENTS.** We thank Dr. Rick Adams and Dr. Rui Costa for advice and discussion. This work was supported by the European Research Council Advanced Grant HUMVOL (Grant 323943). P.H. was additionally supported by a Professorial Research Fellowship from the Economic and Social Research Council.

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