

Differences Between Intention-Based and Stimulus-Based Actions

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Abstract. Actions carried out in response to exogenous stimuli and actions selected endogenously on the basis of intentions were compared in terms of their behavioral (movement timing) and electrophysiological (EEG) profiles. Participants performed a temporal bisection task that involved making left or right key presses at the midpoint between isochronous pacing signals (a sequence of centrally-presented letters). In separate conditions, the identity of each letter either (1) prescribed the location of the subsequent key press response (stimulus-based) or (2) was determined by the location of the preceding key press, in which case participants were instructed to generate a random sequence of letters (intention-based). The behavioral results indicated that stimulus-based movements occurred earlier in time than intention-based movements. The EEG results revealed that activity reflecting stimulus evaluation and response selection was most pronounced in the stimulus-based condition, whereas activity associated with the general readiness to act was strongest in the intention-based condition. Together, the behavioral and electrophysiological findings provide evidence for two modes of action planning, one mediated by stimulus-response bindings and the other by action-effect bindings. The comparison of our results to those of an earlier study (Waszak et al., 2005) that employed spatially congruent visuo-motor mappings rather than symbolic visuo-motor mappings suggests that intention-based actions are controlled by similar neural pathways in both cases, but stimulus-based actions are not.

Keywords: voluntary action, ERPs, readiness potential, P3

Introduction

Human actions exist on a continuum with regard to whether they are driven endogenously (internally by the agent) or exogenously (externally by the environment). At one end of this continuum lie those actions that are spontaneous and endogenously driven (e.g., singing capriciously when elated). In the middle ground reside endogenously-driven actions that are (more or less) directed toward producing desired effects in the environment (e.g., singing a nursery rhyme to entertain a child) as well as exogenously-driven actions that are nonetheless voluntary (e.g., clapping along once the child takes up the tune). We refer to these actions as intention-based and stimulus-based, respectively. Finally, there are involuntary exogenously-driven actions (e.g., the child crying when your overenthusiastic clapping disrupts his or her performance).

The middle ground of the endogenous-exogenous continuum – actions that are both intention- and stimulus-based – has been explored in empirical studies addressing the concepts of voluntary, intentional, or willed actions. Some of this work is clinically motivated, targeting the functional neuroanatomy underlying phenomena such as the illusion of alien control in schizophrenic patients and

akinesia in Parkinson's disease (e.g., Jahanshahi & Frith, 1998; Spence et al., 1997). Other research on the intentionality of actions is motivated by philosophical concerns related to the subjective experience of free will (e.g., Haggard, Clark, & Kalogeras, 2002; Libet, Curtis, Gleason, Wright, & Pearl, 1983).

Most studies on volitional action concern actions that, although voluntary and intentional, are unrepresentative of everyday goal-directed behavior. For example, simply flexing one's index finger at will (Libet et al., 1983) is not particularly high in goal-directedness. In contrast, most real-world intentional actions are carried out to produce desired effects in the environment. Understanding the relationship between actions and the representation of their desired effects has long been the subject of theorizing in philosophical psychology (e.g., James, 1890; Lotze, 1852). Recently, there has been a proliferation of empirical studies that seek to understand how the cognitive system links voluntary motor actions with their intended perceptual effects (e.g., Elsner & Hommel, 2001; Koch & Kunde, 2002; Kunde, 2001; for a review, see Hommel, Müsseler, Aschersleben, & Prinz, 2001).

A view that has found considerable support in this research is the ideo-motor approach to action control. According to the ideo-motor approach, intention-based ac-

tions arise automatically through the anticipation of their sensory effects (James, 1890; Prinz, 1987). Thus, mental representations of intended or goal action effects are responsible for the planning and execution of the appropriate movements for bringing about the goal (e.g., Greenwald, 1970; Prinz, 1997). It has been argued that this action-effect interdependence occurs because the underlying perceptual and motor codes are integrated, or bound together, in a common representational domain (Hommel, 2003; Hommel et al., 2001; Prinz, 1987). Such binding ensures that a combined action-effect representation is activated when an individual imagines a desired goal effect, that is, when he or she has the intention to act.

On the other hand, stimulus-based action has been extensively studied in reaction time experiments. It has been demonstrated that when participants are required to respond to certain stimuli with specific responses, temporary bindings between pertinent stimulus attributes and corresponding action attributes are created and appropriate actions are subsequently selected (e.g., Hommel, Pösse, & Waszak, 2000; Waszak, Hommel, & Allport, 2003). In a broader perspective, these bindings and their underlying condition-action rules reflect the participant's prior stimulus-response learning history. If these bindings are stored in memory, they may serve to guide action on subsequent occasions (cf. Allport, 1987; Logan, 1988; Waszak et al., 2003).

Behavioral Studies of Intention-Based and Stimulus-Based Actions

Consistent with the notion of combined stimulus-response representations and combined action-effect representations, Haggard (Haggard, Aschersleben, Gehrke, & Prinz, 2002; Haggard, Clark, & Kalogeras, 2002; hereafter Haggard et al., 2002a, b, respectively) found that stimuli and responses, on the one hand, and responses and their effects, on the other hand, are perceptually attracted to one another in time. In one study, Haggard et al. (2002a) employed an augmented version of the Libet clock paradigm (Libet et al., 1983; also see Libet, 1985). In the original Libet clock paradigm, participants were instructed simply to move a finger whenever they feel like doing so. While carrying out these voluntary endogenous movements, the participants were required to watch a revolving spot on a numbered clock face and to note and later report the time at which they felt the urge to make each movement. Similarly, Haggard et al. (2002a) required participants to estimate the time at which they performed a prescribed motor act (a key press) and/or perceived an auditory event (a tone), but their participants did so under several experimental conditions. In one (*intention-based action*), participants were instructed to press a response key at will. However, each key press (action) triggered a tone (effect), and participants were required either to judge when they pressed the key or (equally

often) when they heard the tone. In another (*stimulus-based action*) condition, tones were presented at random times and participants were required to react to each tone by pressing the response key. Once again, participants estimated when the key was pressed or the tone was heard. Finally, in two control conditions, participants either only made key presses or only heard tones and made the corresponding time estimates. Haggard et al. (2002a) found that key presses were judged to have occurred later and tones were judged to have occurred earlier in the intention-based condition than in the corresponding control conditions. In other words, time estimates of actions and their effects shifted toward one another. Furthermore, in the stimulus-based condition, time estimates for tones and key presses moved in the opposite direction to those in the intention-based condition, suggesting that the perceptual onset times of stimuli (tones) and their ensuing responses (key presses) were drawn together. The temporal attraction observed in the intention-based and the stimulus-based conditions was taken to support the notion of representational binding, as assumed in the ideo-motor framework.

Importantly for the concept of the subjective experience of free will, the temporal attraction between actions and their effects appears to be contingent upon the actions being voluntary. Haggard et al. (2002b) demonstrated that temporal attraction is reversed, – thus, becoming temporal repulsion – when “effects” (tones) are triggered by transcranial magnetic stimulation (TMS) of the motor cortex (which induces involuntary muscle twitches) rather than by intentional, self-paced, key presses. This finding suggests that action-effect binding may be the mechanism behind the experience of one's own causal agency: Events that match the anticipated effects of an action are attributed to the self, whereas events that do not match such predictions are attributed to an external source (see Frith, 1992). More specifically, it may be the activation of combined action-effect representations that leads to the conscious awareness of the intention to act (see Haggard et al., 2002b). If so, intention-based and stimulus-based actions should differ not only in behavioral indices, such as temporal attraction measures, but also in terms of their electrophysiological signatures.

Electrophysiological Signatures of Intention-Based and Stimulus-Based Actions

A large body of electrophysiological research has examined movement-related potentials that are purported to be the antecedents of intention-based actions. One of the most vigorously studied of these EEG components is the *readiness potential* (RP) – a slow negative cortical potential associated with the preparation and initiation of self-paced movements (Kornhuber & Deecke, 1965; Libet et al., 1983). The results of work with such potentials and related neurophysiological research suggest that intention-based

actions are mediated by frontostriatal circuits involving the dorsolateral prefrontal cortex, the anterior cingulate, and the supplementary motor area (SMA; Deecke & Lang, 1990; Goldberg, 1985). On the other hand, the most strongly implicated brain area for movement control in the context of stimulus-based actions is the lateral premotor cortex (Passingham, 1985; Thut et al., 2000). Stimulus-based actions are typically characterized by a centroparietal positivity about 300 ms after stimulus presentation (the P3 response), which may reflect the formation of a link between stimulus processing and response planning (e.g., Verleger, Jaskowski, & Wascher, 2005).

Waszak et al. (2005) compared the functional signatures of intention-based and stimulus-based actions by examining both behavioral (temporal attraction) and electrophysiological (EEG) measures. The experimental task involved making key presses at the midpoint between adjacent items in evenly timed sequences of visually-presented pacing signals. The signals were presented with a 1200 ms intersignal interval (ISI) at locations on a computer screen that corresponded to the spatial layout of the keys on a response box. In an intention-based condition, participants were instructed to make whatever key press they wished, and the identity of each key press determined the location of the subsequent signal. In a stimulus-based condition, the signals served as stimuli: Participants were required to press the key that corresponded to the spatial location of the immediately preceding signal. The movements in a given stimulus-based run were yoked (in a disguised fashion) to the movements produced in a preceding intention-based run. Thus, Waszak et al. (2005) were able to compare the movement timing and EEG profiles of physically identical actions under conditions where they were performed either in an intention-based or stimulus-based mode.

In their behavioral data, Waszak et al. (2005) observed temporal attraction effects in the timing of movements. Specifically, they found that key presses, which generally preceded the true ISI bisection point by about 80 ms on average, occurred about 50 ms earlier in the stimulus-based condition than in the intention-based condition. Thus, consistent with the notion of perception-action binding, and analogous to the perceptual effects found by Haggard et al. (2002a, b), intention-based actions occurred relatively close in time to their anticipated effects, whereas stimulus-based actions occurred closer to their triggering stimuli.

Waszak et al. (2005) also focused on several EEG components, including stimulus-locked and response-locked ERPs and LRPs, to gain insight into the electrophysiological signatures of intention-based vs. stimulus-based actions. With regard to stimulus-locked ERPs, Waszak et al. observed two EEG components that were present approximately 200–400 ms after stimulus presentation only in the stimulus-based condition: A centro-parietal P3 and a fronto-central S-LRP (stimulus-locked lateralized readiness potential). Waszak et al. argued that these two components reflect stimulus-driven stimulus-response binding processes that take effect whenever specific movements are

to be carried out in response to specific stimuli (see also Verleger et al., 2003).

Waszak et al. (2005) also observed increased negativity contralateral to the side of the stimulus over sensory, parietal, and motor areas in the N1 range. They suggested that these asymmetries reflected different aspects of automatic sensory-motor integration, including visual selection, mapping of the visuo-spatial attributes onto motor responses in parietal areas, and visuo-spatial processing for response selection in lateral premotor areas (see also Iacoboni, Woods, & Mazziotta, 1996; Praamstra & Oostenveld, 2003; Wascher, Reinhard, Wauschkuhn, & Verleger, 1999). Asymmetries over parietal areas related to stimulus-response mapping and response-related asymmetries over motor areas were more pronounced for stimulus-based actions than for intention-based actions, suggesting that stimuli were processed right up until response activation only, or to a larger degree, if the stimuli were relevant for the upcoming movement.

Waszak et al. (2005) also found a complementary pattern of activity in the response-locked ERPs. They observed a more pronounced negative shift before movements in intention-based conditions than in stimulus-based conditions. The authors pointed out that although this component resembled the RP, the difference in premovement negativity between the two conditions had to be interpreted cautiously because it was similar to the difference in P3 activity in terms of magnitude and topography. Thus, it was not fully resolved whether the differences in EEG activity for intention-based and stimulus-based actions were related to (1) action planning and/or action-effect anticipation in the intention-based conditions, (2) evaluating the stimulus and invoking the appropriate response rule in the stimulus-based conditions, or (3) a combination of these processes.

The Current Study

The current study was designed as an extension of the work of Waszak et al. (2005), and, as such, employed a similar temporal bisection task. Our first aim was to test how the behavioral and electrophysiological phenomena from Waszak et al. (2005) generalize from the spatial domain to a more abstract symbolic domain (cf. Koch & Kunde, 2002). To this end, we eliminated the spatial component of the stimuli/effects by using a pacing sequence composed of centrally-presented, symbolic signals (letters presented at fixation). It was important to explore symbolic signals for two reasons.

First, it is unclear whether the attraction effects demonstrated by Haggard and colleagues (Haggard et al., 2002a, b) and by Waszak et al. (2005) can be observed with arbitrary stimulus-response and action-effect mappings. Many human activities, such as musical performance, involve such arbitrary mappings. Second, the comparison of spatial vs. symbolic visuo-motor transformations may prove valuable in light of recent claims that visual information can

reach the motor system through different, task-dependent pathways (Passingham, Toni, & Rushworth, 2000; Toni, Rushworth, & Passingham, 2001). Passingham and colleagues suggested that visual information flows through the dorsal system when visual stimuli spatially direct movements toward the target of an action. The functional anatomy subserving such spatially congruent visuo-motor transformations most likely includes a cerebral circuit with contributions from portions of the inferior parietal cortex, anterior intraparietal area, and ventral premotor cortex (Fogassi et al. 2001; Gallese et al. 1994; Luppino et al. 1999; Rizzolatti et al. 1988; Sakata et al. 1995). The results of Waszak et al. (2005) are consistent with the notion that this dorsal pathway mediates spatially congruent visuo-motor transformations. According to Passingham and colleagues, a different pathway that involves the ventral stream, and extends into the ventral prefrontal cortex, is recruited when visual stimuli demand that a decision be made about which of several alternative actions to perform, as is the case in the present study. If this hypothesis is correct, one would expect that the early-onset stimulus-locked lateralized activity over motor, parietal, and visual areas, and the late-onset S-LRP, observed by Waszak et al., should not be observed here.

The second aim of the current study was to clarify whether the differences in stimulus-locked and response-locked ERPs observed by Waszak et al. (2005) for intention-based and stimulus-based actions were mainly attributable to differences in stimulus evaluation or to differences in movement planning for the two types of action. To shed light on this matter, we used two different ISI values: 1200 ms and 1600 ms. Whereas stimulus processing may still be in progress at the temporal bisection point (600 ms) of the short ISI (1200 ms), it should be less active before the bisection point (800 ms) of the long ISI (1600 ms). By this reasoning, it should be possible to measure processes related mainly to movement initiation prior to the bisections in the long ISI condition.

Method

Participants

Ten participants (9 females, 1 male) took part in the experiment. Their ages ranged from 18 to 34 years. All participants were right-handed, naive with regard to the purpose of the experiment, and paid in return for participation. No participant reported a history of neurological disease and all gave their informed consent to participate.

Apparatus and Stimuli

The experiment took place in a dimly-lit, sound-attenuated room. Participants sat, wearing headphones, in a dentist-

style chair in front of a computer screen. A keyboard with two response keys separated by a horizontal distance of 13.5 mm was positioned on a tray at a comfortable height and distance in front of the participant. Visual signals consisted of the letters O, X, and H ($1.2^\circ \times 1.2^\circ$ degrees of visual angle) presented at the center of the computer screen. In addition, an auditory pacing signal composed of a sine tone (600 Hz; 100 ms in duration) was presented at the start of each data collection run (see below) through the headphones at a comfortable loudness (60 dBA). An IBM-compatible computer in a room adjoining the sound-attenuated room controlled the presentation of stimuli and collected behavioral data with accuracy better than 1 ms.

EEG was recorded from 60 Ag/AgCl electrodes distributed over the entire scalp, with an electrode affixed at Cz for reference. To control for ocular artifacts, the electro-oculogram (EOG) was recorded both vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). EEG and EOG were amplified and filtered by two Synamps (Neuroscan) DC-amplifiers (0–100 Hz bandpass). EEG and EOG were digitized at 500 Hz and stored simultaneously on a second computer. EEG was re-referenced to linked mastoids and was corrected offline for eye movements (see Gratton, Coles, & Donchin, 1983) and other artifacts.

Design

A 2×2 repeated measures design was employed, with factors *action* (intention-based vs. stimulus-based) and *ISI* (1200 vs. 1600). The dependent variables are described after the Procedure section.

Procedure

Each participant came for a single session that lasted approximately 3 h, including the time required to fix the EEG electrodes and to practice and complete the task. After the electrodes were affixed to the participant's scalp, he or she was given verbal instructions about the task and the opportunity to practice temporal bisection. In this practice phase, the participant pressed either one of the two response keys (in random order) so as to bisect the temporal intervals defined by a visual metronome consisting of a ' + ' symbol that appeared for 200 ms periodically at the center of the computer screen. The ISI during this practice phase was set at 1200 ms. The left and right keys were pressed with the left and right index fingers, respectively. Feedback concerning the accuracy of performance was provided in the form of a horizontal bar that appeared to the left or to the right of the center of the computer screen, depending on whether each key press was made earlier or later than the true bisection point. Furthermore, the length of the bar was directly proportional to the magnitude of the timing error. The practice phase ended when the participant indicated

that he or she was confident in his or her ability to perform the temporal bisection task.

The experiment itself consisted of two blocks of 40 runs. The ISI factor was varied between blocks and the action factor was varied within blocks such that intention-based runs alternated with stimulus-based runs. In both types of runs, the participant was required to make key press movements at the midpoint between adjacent items in an evenly-timed run of 35 visually-presented letters (Os and Xs). Each letter appeared for 200 ms at the center of the computer screen. The ISI was 1200 ms for runs in the first block and 1600 ms for runs in the second block or vice versa (counterbalanced across participants). The bisection points at which participants were supposed to make key presses were located 600 ms following the onset of each letter in the 1200 ms ISI condition and 800 ms following letter onsets in the 1600 ms ISI condition.

In intention-based runs, the identity of the key (left or right) that was pressed during each ISI determined the identity of the subsequent letter (O or X). Participants were instructed to make key presses at the bisection point of each ISI so as to produce a random sequence of letters. In the stimulus-based runs, the order of the letters in the stimulus sequence was predetermined and the participant was required to press the key that corresponded to the immediately preceding stimulus (left in response to O and right in response to X). To maintain the same degree of left-right movement alternation in both conditions, the letter sequence in a given stimulus-based run was yoked to the letter sequence produced by the participant in the last but one intention-based run (except for the first stimulus-based run, for which a random stimulus sequence was generated by the computer). To prevent subjects from gaining insight into this coupling of runs, sequences (a) were inverted, i.e., Os were replaced by Xs and vice versa, and (b) were presented in reversed order. In addition, to allow us to verify whether the participant was attending to the stimuli during both the intention-based runs and the stimulus-based runs, 1% of the target letters (Os and Xs) within each block were replaced randomly by a catch stimulus letter (H). The participant was instructed to stop tapping immediately upon presentation of a catch signal. (Participants generally had little trouble with this task, although some were caught out occasionally in the 1200 ISI condition.)

To assist participants in the temporal bisection task, an auditory pacing signal marked the true ISI midpoint for the first 10 ISIs of each run. Participants were required to synchronize key presses with the tones of this pacing signal and then, once the auditory pacing signal ceased, to maintain this anti-phase relationship with the letter sequence for a further 24 ISIs (plus a key press following the last stimulus item in each run). Runs were cancelled and repeated when the timing of the key press deviated by more than ± 350 ms from the true bisection point. Before data collection began, participants were allowed to practice the intention-based and stimulus-based runs (typically twice each, interleaved).

Data Analysis

Behavioral Data

Accuracy at the temporal bisection task was assessed by measuring the asynchrony (in ms) of each key press from the true midpoint of the ISI during which it was made. Data collection started with the onset of the 16th ISI (i.e., five key presses after the auditory pacing signal ceased) in each run. Asynchronies that fell within ± 350 ms of the true bisection point were then averaged separately for each experimental condition. We expected our experimental task to be more difficult than the task used by Waszak et al. (2005) because it employed symbolic centrally-presented, rather than spatial, stimuli. The mapping between stimuli and responses (in the stimulus-based condition) and actions and effects (in the intention-based condition) was arbitrary, and, as such, probably required learning. To assess the learning, we divided runs into those that occurred within the first half (runs 1–10) and the second half (runs 11–20) of each ISI block. Finally, the resultant mean asynchronies for each participant were analyzed in a 2 (block half: First or second) \times 2 (action) \times 2 (ISI) analysis of variance (ANOVA) with the criterion for statistical significance set at $\alpha = .05$.

Electrophysiological Data

Both stimulus-locked and response-locked ERPs were examined, the former being time locked to the onset of the stimulus (visually-presented O or X), the latter being time locked to the onset of the response (key press). The P3 component was indexed by the mean amplitude within the 300–400 ms range of the stimulus-locked averages. For analysis, mean amplitudes in a representative electrode grid (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) were entered into a 2 \times 2 \times 3 \times 3 ANOVA with the factors action condition (intention based vs. stimulus based), ISI (1200/1600 ms), anterior-posterior topography (anterior/center/posterior), and lateral topography (left/center/right). Response-locked averages (i.e., mean amplitudes within the last 200 ms preceding the response) were analyzed in an ANOVA of similar design. The block-half factor was not included in these analyses because visual inspection revealed no qualitative differences between data from each half of the blocks.

Event-related lateralizations of the EEG were calculated for the electrode pairs FC3/FC4 (i.e., the electrode positions in a regular 10/20 system that are closest to the hand motor areas) and P7/P8, where attentional effects are most pronounced, by subtracting the EEG activity ipsilateral to the movement from the activity contralateral to the movement. Separate difference waves for left and right movements were averaged to compute the LRP (cf. Gratton et al., 1988). Response-locked LRPs were indexed by the mean amplitude within the last 50 ms preceding movements.

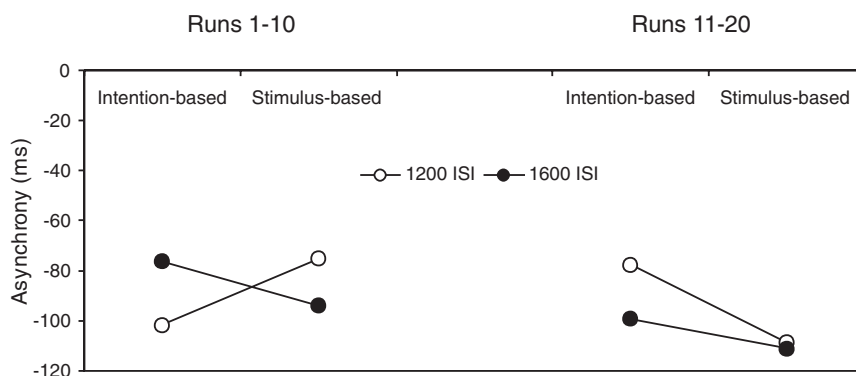


Figure 1. Mean asynchronies (in ms) in intention-based and stimulus-based action conditions in the first half (runs 1–10) and second half (runs 11–20) of each ISI (1200 ms or 1600 ms) block.

Finally, to allow our results to be compared to those of Waszak et al. (2005), we examined activity in the N1 range over sensory, parietal, and motor areas. (In contrast to Waszak et al., we did not expect to find any such activity to be reliable.) First, at electrode pairs P7/8, P3/4, and C1/2, early lateralization was examined by measuring the most negative peak in the stimulus-locked lateralizations 120–220 ms after stimulus onset. These data were subjected to an ANOVA including the factors action condition (intention-based vs. stimulus-based), ISI (1200/1600 ms), and electrode (P7/8, P3/4, and C1/2). Second, S-LRP amplitudes were measured for the electrode pair FC3/FC4 between 230 ms and 360 ms after stimulus onset. An ANOVA including the factors action condition and ISI was run to evaluate these data. Note that because our stimuli were centrally presented, in contrast to the lateralized stimuli used by Waszak et al. (2005), the above EEG lateralizations were computed relative to the response location prescribed by the identity of each stimulus.

Results

Behavioral Data

The mean asynchronies of movements from the true bisection point in the two action conditions and the two ISI conditions are shown in Figure 1, with means from the first half of each ISI block shown on the left and means from the second half of the block shown on the right. It can be seen that movements generally preceded the true bisection point. (For a discussion of such “negative asynchronies” in sensorimotor synchronization tasks, see Aschersleben, 2002.) Although the ANOVA for these asynchronies yielded no main effects of the action variable or the ISI variable or the block-half variable, $F_s(1, 9) < 1$, there was a significant interaction between the action variable and the block half variable, $F(1, 9) = 14.67, p < .01$. *Post hoc* compari-

sons revealed that movements occurred significantly later in the intention-based condition (mean asynchrony = –88 ms) than in the stimulus-based condition (mean asynchrony = –110 ms) in the second half of each block, $F(1, 9) = 7.34, p < .025$, but not in the first half (–89 and –84 ms, respectively), $F(1, 9) < 1$. Thus, a temporal attraction effect similar to that observed by Waszak et al. (2005) was found here, but only after participants had considerable practice at the task.¹

Electrophysiological Data

Stimulus-locked ERP averages for frontal, central, and posterior midline electrodes are shown in Figure 2, where it can be seen that the P3 complex (spanning roughly the 300–400 ms range) was manifest only in the stimulus-based condition, as evidenced by a significant effect of the action factor, $F(1, 9) = 5.26, p < .05$. This finding, which is consistent with the results of Waszak et al. (2005), suggests that the pacing signals captured attention to a greater degree when they served as stimuli that provided information about which key to press than when they served as action effects. The P3 effect was most pronounced at Cz, as evidenced by a significant three-way interaction between action, anterior-posterior topography (quadratic trend contrast: Central vs. frontal and posterior combined), and lateral topography (quadratic contrast: Central vs. left and right), $F(1, 9) = 9.85, p < .02$. There were no significant main effects of ISI, frontal-posterior topography, or lateral topography on P3 amplitude, and no significant interactions between these factors and the action factor, $ps > .08$.

The corresponding response-locked ERPs (R-ERPs) are shown in Figure 3. Recall that Waszak et al. (2005) could not be sure whether the R-ERP component that they observed reflected stimulus-related or response-related processes, because movements were executed soon after the

¹ Closer inspection of Figure 1 suggests that the unexpected effect during the first half of each block was confined to the 1200 ms ISI condition, where movements occurred later in stimulus-based runs than in intention-based runs. This reversal of the predicted effect – although not in itself statistically significant, $p > .2$ – may reflect an initial slowness of responding in the stimulus-based condition caused by difficulties associated with the arbitrary stimulus-response mapping. It makes sense to expect that such slowness would be less costly at the 1600 ms ISI, where the relatively late location of the true bisection point allowed more time for stimulus evaluation and response planning.

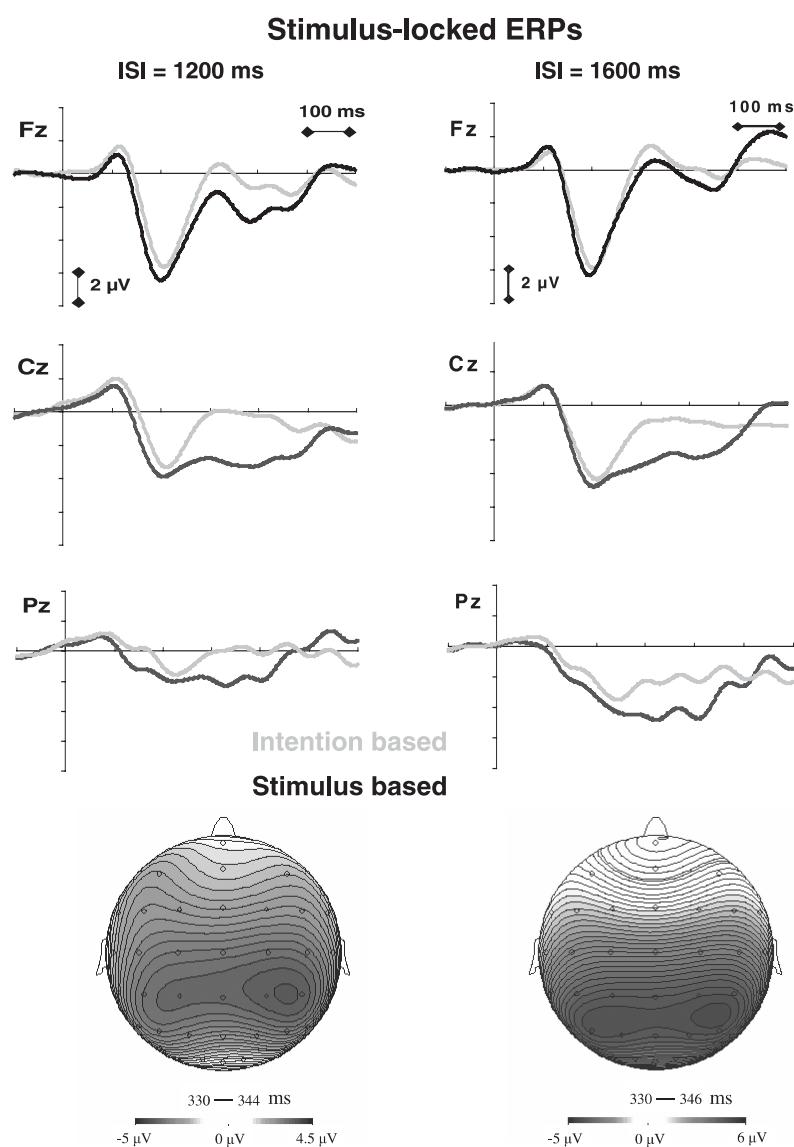


Figure 2. Stimulus-locked ERPs in intention-based and stimulus-based action conditions at the 1200 ms ISI (left panels) and 1600 ms ISI (right panels). Time (in ms; 0 = stimulus onset) is shown on the horizontal axis and amplitude (in μV ; positive down) is shown on the vertical axis. Topographical maps of the main stimulus-locked ERP peaks (corresponding to the P3) for *stimulus-based actions* in the two ISI conditions are shown at the bottom of the figure.

spacing signals (within 600 ms of the 1200 ms ISI) in their task. (Response-related processes are of greater theoretical interest as a result of their relation to the RP.) We sought to resolve this issue by using both a long ISI (1600 ms) and a short ISI (1200 ms). Stimulus processing may still be very much in progress at the temporal bisection point (600 ms) of the short ISI, but should be less active for the last 200 ms before the bisection point (800 ms) of the long ISI. If so, the difference in R-ERP amplitude during the 200 ms preceding responses for intention-based and stimulus-based actions should be larger in the short ISI condition than in the long ISI condition.

The analysis of our R-ERP data revealed a significant main effect of action condition, $F(1, 9) = 11.67, p < .01$, as well as a significant interaction between action and ISI, $F(1, 9) = 11.7, p < .01$. Although R-ERP amplitudes were generally larger in the intention-based condition than in the stimulus-based condition, this difference was more pro-

nounced at short than at long ISIs. This interaction is inconsistent with the notion that these components only reflect response-related processes in both ISI conditions. In light of this, it seemed likely that stimulus-related processes contributed to the R-ERP differences in the 1200 ISI condition. Consequently, we decided to focus on R-ERPs in the 1600 ms ISI condition. We assumed that, within this condition, activity occurring prior to the last 200 ms preceding movements reflected a mixture of stimulus- and response-related processes, but activity during the last 200 ms before movements was a relatively pure index of response-related processes, possibly comprising the tail end of the RP. Consistent with this expectation, in this region we found that mean R-ERP amplitude was larger for intention-based movements than for stimulus-based movements, $F(1, 9) = 11.04, p < .01$. To the extent that this constitutes a difference in RPs, it may be taken as evidence for differences in the general preparatory processes that lead

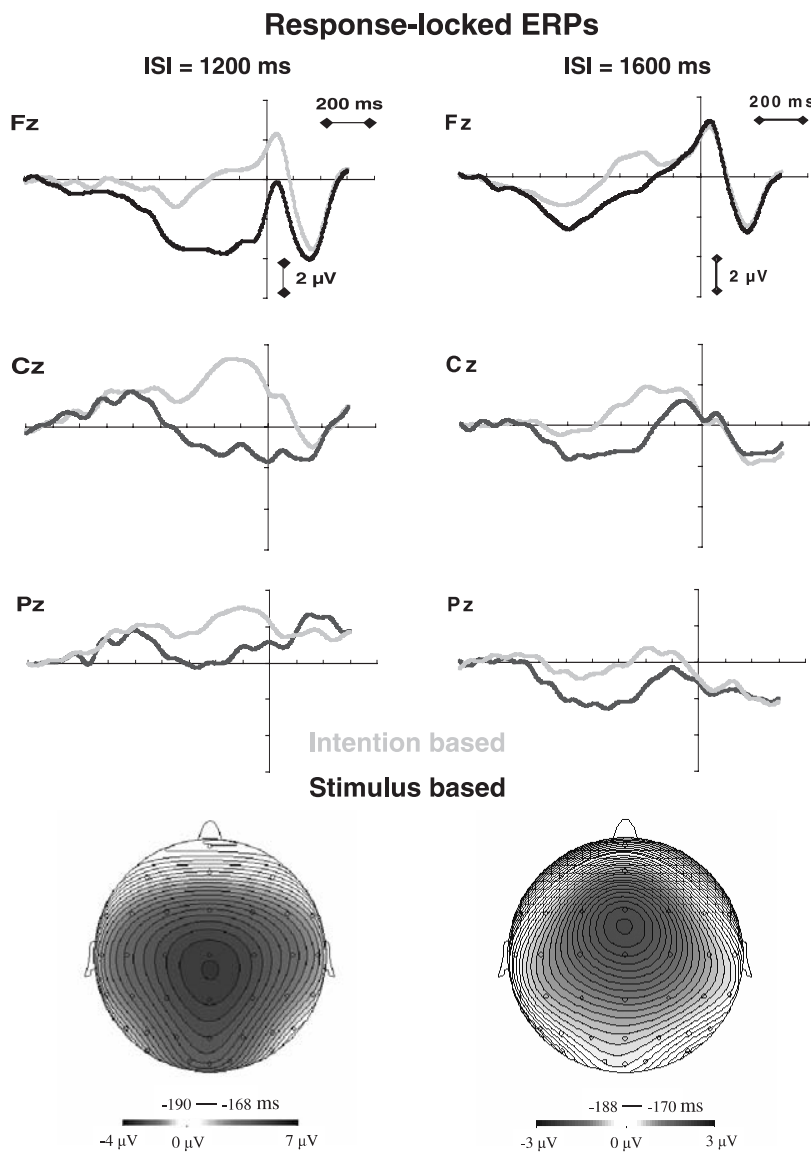


Figure 3. Response-locked ERPs in intention-based and stimulus-based action conditions at the 1200 ms ISI (left panels) and 1600 ms ISI (right panels). Time (in ms; 0 = time of key press) is shown on the horizontal axis and amplitude (in μV ; positive down) is shown on the vertical axis. Topographical maps of the main response-locked ERP peaks (which may correspond to the RP) for *intention-based actions* in the two ISI conditions are shown at the bottom of the figure.

to intention-based vs. stimulus-based actions. Furthermore, this effect of action mode was not affected reliably by anterior-posterior topography, $F(2, 18) = 1.62, p > .2$. The latter result may suggest that the readiness for action was manifest across motor and sensory areas. The topographical map at the bottom right of Figure 3 shows that intention-based R-ERP activity in the 1600 ms ISI condition has a fronto-central maximum. The different appearance of the map for the 1200 ms ISI condition (at the bottom left of the figure) may be caused by overlapping stimulus-related and response-related components at the shorter ISI.

We turn now to lateralized cortical activity. Figure 4 shows stimulus-locked and response-locked lateralized activity recorded over hand motor areas. As expected, there was no evidence for reliable differences in early-onset stimulus-locked lateralized activity over motor areas for intention-based vs. stimulus-based actions. In addition, there were no significant early-onset stimulus-locked lateraliza-

tions over visual or parietal areas (not shown in Figure 4), and there was no reliable late S-LRP. Thus, the use of centrally-presented stimuli effectively neutralized the lateralized EEG activity that Waszak et al. (2005) observed with spatial stimuli.

Response-locked LRPs (mean amplitude during the last 50 ms preceding movements) did not differ reliably between intention-based and stimulus-based conditions, $p > .1$. Thus, as found by Waszak et al. (2005), the time course of motor preparation was similar for intention-based and stimulus-based actions. Furthermore, although the main effect of ISI on lateralized activity approached significance, $F(1, 9) = 4.21, p = .07$, perhaps reflecting a slight difference in the time course of preparation for movements at fast and slow rates, the interaction between ISI and action was far from significant, $p > .4$. Analyses of LRP onset latencies revealed no significant differences between intention-based and stimulus-based actions.

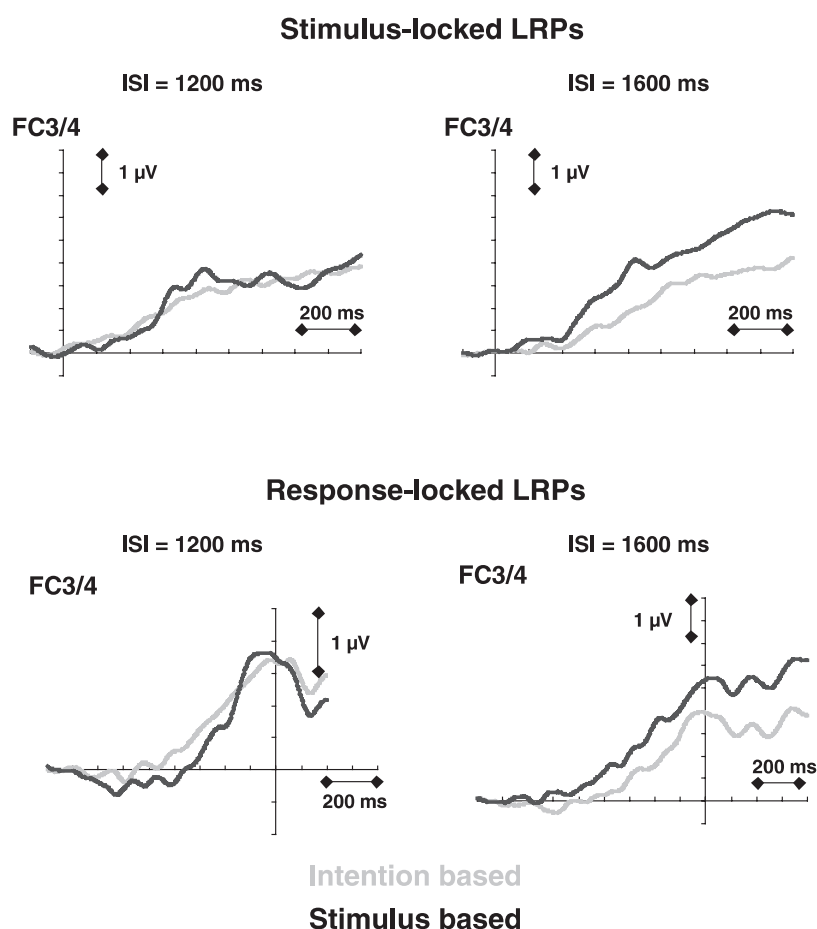


Figure 4. Stimulus-locked LRPs (top panels) and response-locked LRPs (bottom panels) in intention-based and stimulus-based action conditions at the 1200 ms ISI (left panels) and the 1600 ms ISI (right panels). Time is shown on the horizontal axis and amplitude (in μV ; positive down) is shown on the vertical axis.

Discussion

In the present study, we compared intention-based actions and stimulus-based actions with respect to their behavioral and electrophysiological profiles. The experimental paradigm was a temporal bisection task in which participants were asked to make key presses at the midpoint between isochronous pacing signals. As found with a similar task in an earlier study (Waszak et al., 2005), we observed that movements occurred earlier for stimulus-based actions than for intention-based actions. This temporal attraction effect (which emerged only when the arbitrary stimulus response mapping had been learned) is a motor timing analog of the perceptual attraction effects observed by Haggard et al. (2002a, b). As such, it accords with the notion, derived from the ideo-motor framework, that sensory-motor linkages take the form of compound representations incorporating stimuli and responses on one hand and actions and effects on the other hand.

The stimulus-locked ERP data also provided evidence for stimulus-response binding. Specifically, the finding that the P3 component was larger in stimulus-based than in intention-based conditions suggests that attentional processes formed a more active link between pacing signals and subsequent movements when the signals specified how to

act than when the signals merely echoed what act was just performed. This link presumably served to guide the processes of transforming sensory information into the associated response. In this regard, our results extend the results of Waszak et al. (2005) because the current version of the temporal bisection task used centrally presented symbolic stimuli to specify left or right responses rather than spatial stimuli that corresponded to the response locations. Thus, the current findings demonstrate that the stimulus-response binding effect found by Waszak et al. (2005) generalizes from a relatively concrete (spatial) domain to a more abstract (symbolic) domain, and so is a general phenomenon of sensory-motor transformations.

The present study also yielded evidence that action-effect binding plays a role in planning intention-based actions. This evidence was in the response-locked ERPs, where we observed that a negative peak preceding movements was more pronounced for intention-based actions than for stimulus-based actions. Waszak et al. (2005) observed a similar difference in ERP amplitudes but were hesitant to draw strong conclusions about its source because the relatively short ISI in their task made it possible that the previous pacing signal was still being processed at the time movements were being made. We attempted to circumvent this problem here by using both short and long ISIs. Finding that the premovement negativity was still

greater for intention-based actions than for stimulus-based actions at the long ISI suggests that this negative activity represents the final stages of the RP (see Deecke & Lang, 1990). Therefore, the differences in premovement negativity that we observed between the two action conditions can be taken as evidence that the planning of intention-based actions involves enhanced cortical preparation relative to the planning of stimulus-based actions. The observation that this apparent readiness for action was distributed across motor and sensory areas may be taken as evidence for action-effect binding, although this inference can be drawn only tentatively until future research with source estimation methods is undertaken. Nevertheless, our interpretation squares with the well-supported concept from ideomotor theory that the planning of intention-based actions involves the anticipation of the sensory consequences of those actions (see Prinz, 1997). Our finding that the relatively strong R-ERPs for intention-based actions were located centrally is also consistent with claims that the SMA plays a special role in voluntary movement control (see Deecke & Lang, 1990).

To the extent that the topography of scalp ERPs roughly corresponds to the spatial distribution of cortical activity, the present data also bear on the neural circuitry for visuo-motor transformations, though, once again, our claims must be tentative in this regard. As mentioned in the introduction, spatially congruent visuo-motor transformations, on the one hand, and arbitrary visuo-motor transformations, on the other hand, are considered to be controlled by different pathways – dorsal and ventral, respectively (Passingham et al., 2000; Toni et al., 2001). Another body of work suggests that spatially directed actions rely on a circuit involving the inferior parietal cortex, the anterior intraparietal area, and the ventral premotor cortex (Fogassi et al. 2001; Gallese et al. 1994; Luppino et al. 1999; Rizzolatti et al. 1988; Sakata et al. 1995). Consistent with this hypothesis, Waszak et al. (2005) observed a centro-parietal P3 and fronto-central lateralizations (S-LRPs) following stimulus presentation in their stimulus-based action condition, but not in their intention-based condition. Waszak et al. also observed increased negativity for stimulus-based relative to intention-based actions in several areas contralateral to the side of the stimulus presentation.

As observed by Waszak et al. (2005), we found a parietal P3 that was much larger in the stimulus-based condition than in the intention-based condition. However, in contrast to Waszak et al., we found no evidence for early-onset stimulus-locked lateralized activity over visual, parietal, or motor areas, and no reliable late S-LRP. The absence of lateralizations over sensory areas presumably occurred as a re-

sult of our use of centrally-presented stimuli. More interestingly, lateralizations over parietal areas were absent presumably because, in contrast to spatially congruent visuo-motor transformations, parietal areas are not involved in arbitrary transformations (Passingham et al., 2000; Toni et al., 2001). We believe that lateralizations over motor areas were not observed here because, as proposed by Passingham and colleagues, the dorsolateral and not the ventrolateral premotor cortex is involved in arbitrary visuo-motor transformations. Indeed, it has been shown that a major component of activity in the dorsolateral premotor cortex represents movement in a more abstract, or task-dependent and effector-independent, manner (Cisek, Crammond, & Kalaska, 2003).

Considering all our results alongside those of Waszak et al. (2005), it appears that the dorsal system makes use of spatial codes to process stimuli until response activation only in the case of congruent spatial visuo-motor transformations. The dorsal system is not implicated in the same way with arbitrary transformations presumably because there is no direct spatial correspondence between stimulus and response that can be used to guide the movement. Hence, stimuli and responses must be represented at a relatively high cognitive level, which probably involves “cross-domain mapping” (Wise, Pellegrino, & Boussaoud, 1996), thought to be achieved through a pathway including the ventral stream, the ventral prefrontal cortex, and the dorsolateral premotor cortex (Passingham et al., 2000; Toni et al., 2001). Within this pathway the ventral prefrontal cortex may set up an “attentional template” for stimuli and their unique features in the infero-temporal cortex. Such templates may serve both to highlight stimuli that are behaviorally significant (Desimone & Duncan, 1995) and to bias competition between representations of movement in the premotor areas (Frith, 2000).²

To conclude, we have shown that intention-based and stimulus-based actions can differ markedly in terms of their behavioral and electrophysiological signatures even when the actions themselves are outwardly similar. This provides evidence for two distinct mechanisms that mediate the planning of voluntary actions: A stimulus-based (exogenous) mechanism underpinning stimulus-response bindings and an intention-based (endogenous) mechanism that works with action-effect bindings. The similarities between our results and those of Waszak et al. (2005) suggest that intention-based actions recruit similar neural pathways and processes regardless of whether arbitrary visuo-motor transformations or spatially compatible transformations mediate voluntary movements and their effects. The differences between our results and those of Waszak et al. (2005)

2 One might argue that the difference between spatially congruent transformations and arbitrary transformations is a matter of degree, with the former being automatized by the perpetual interaction of the agent with the environment. If so, it would be possible that after a sufficient amount of practice, nonspatial arbitrary stimuli would also automatically activate their associated responses via the same pathway as stimuli that are spatially congruent with the response. However, we analyzed ERPs separately for the last quarter of the experiment and found no reliable lateralizations. This outcome suggests that the difference in the pattern of results between the present study and the Waszak et al. (2005) study reflects differences in functional architecture rather than degree of automatization.

were confined mainly to the EEG signatures of stimulus-based actions, suggesting that such actions are controlled by different neural pathways when stimuli and responses are related through arbitrary visuo-motor transformations (ventral stream) rather than spatially compatible transformations (dorsal stream).

A final comment concerns the subjective experience of the will. Although the current study was not explicitly concerned with this critical aspect of phenomenology, our findings may be seen to address issues relevant to recent discussion of this topic. Wegner (2002) argued that the experience of free will is illusory and stems from the predisposition of the human brain to attribute authorship to the self whenever an action matches a thought that appears in consciousness just prior to the action. Our results suggest that it may be fruitful for future research to explore the idea that the anticipatory activation of combined action-effect representations may constitute such a “thought” and that this activation might be a mechanism that contributes to the awareness (whether true or false) of the will to act.

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