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The real-time link between person perception and action: Brain potential evidence for dynamic continuity

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Using event-related potentials, we investigated how the brain extracts information from another's face and translates it into relevant action in real time. In Study 1, participants made between-hand sex categorizations of sex-typical and sex-atypical faces. Sex-atypical faces evoked negativity between 250 and 550 ms (N300/N400 effects), reflecting the integration of accumulating sex-category knowledge into a coherent sex-category interpretation. Additionally, the lateralized readiness potential revealed that the motor cortex began preparing for a correct hand response while social category knowledge was still gradually evolving in parallel. In Study 2, participants made between-hand eye-color categorizations as part of go/no-go trials that were contingent on a target's sex. On no-go trials, although the hand did not actually move, information about eye color partially prepared the motor cortex to move the hand before perception of sex had finalized. Together, these findings demonstrate the dynamic continuity between person perception and action, such that ongoing results from face processing are immediately and continuously cascaded into the motor system over time. The preparation of action begins based on tentative perceptions of another's face before perceivers have finished interpreting what they just saw.

Keywords: Person perception; Action; Face perception; Social categorization; Motor processes; ERPs.

INTRODUCTION

People glean a variety of information from the faces of others, and such perceptions have consequences. Among the information that is effortlessly read from others' faces are social categories (e.g., "she's a woman"), dispositional characteristics (e.g., "she's intelligent"), and emotional states (e.g., "she's angry"). These spontaneous extractions then trigger a variety of cognitive, affective, and behavioral consequences that shape the likely course of social interaction (Ambady, Bernieri, & Richeson, 2000; Macrae & Bodenhausen, 2000). What remains far less clear, however, is the nature of the relationship between these perceptual extractions and the immediate action that results from them. For instance, upon catching sight of another's face, how is knowledge about that

person's sex gleaned and translated into relevant action? Here we examine how information from another's face is accrued and turned into action in real time.

The link between social perception and action has long been explored in the context of automatic "perception–behavior" associations. This work has generally examined how primes subtly perceived during the earlier part of an experiment influence downstream behavior in a later portion of the experiment. For instance, after participants unobtrusively perceive information about the category, Elder, they begin to walk more slowly (Bargh, Chen, & Burrows, 1996), after perceiving information about the category, Black, they produce more nonverbal hostility (Bargh, Chaiken, Raymond, & Hymes, 1996), and after perceiving information about the category, Professor,

they perform better on general knowledge tests (Dijksterhuis & Van Knippenberg, 1998). Thus, the perception of information about certain social concepts can automatically influence behavior.

But what about more immediate behavior resulting from person perception, such as that occurring in social interaction? How does the perception of another's face translate into relevant actions across just hundreds of milliseconds? Traditional cognitive theories posit that the transformation from perception to action is accomplished by serial non-overlapping processing stages: perception → cognition → action (temporal cortex → "association cortex" → motor cortex; Dietrich & Markman, 2003; Fodor, 1983; Pylyshyn, 1984; Sanders, 1990; Sternberg, 1969). Information impinging on the retina is transmitted to the perceptual system, which collects the information and constructs an internal representation of it (Marr, 1982). Once this is finalized, the perceptual system sends its results on to the cognitive system, which interprets the information and decides on an appropriate course of action (Newell & Simon, 1972). Once the decision is finalized, it is sent on to the motor system, which prepares the planned trajectory of movement and then executes it (Keele, 1968).

Although a serial stage-based framework has been valuable, it has become increasingly clear that cognition does not sharply collapse its processing onto the discrete execution of a bodily movement. Rather, movement is continuously adjusted by cognitive processing over time. Even with saccadic eye movements, which are highly ballistic (itself oft-touted evidence for a discrete transition between cognition and action), the curvature of the saccadic trajectory is influenced by attention to a stimulus's context (Sheliga, Craighero, Riggio, & Rizzolatti, 1997). Moreover, as participants attempt to grab an object that moves while the arm is still in motion, the trajectory of the arm is continuously adjusted in mid-air to seamlessly arrive at the object's new point in space (Goodale, Pelisson, & Prablanc, 1986), and as participants move a finger to point at a target, the finger's trajectory exhibits a temporally dynamic influence from subliminal primes that smoothly alters its curvature (Finkbeiner, Song, Nakayama, & Caramazza, 2008; Schmidt, 2002). In short, the dynamics of action do not simply reside in the aftermath of cognition; rather, they are part and parcel with it, and show systematic covariation (Dale, Roche, Snyder, & McCall, 2008; Song & Nakayama, 2009; Spivey, 2007).

Such findings of cognition–action covariation lend support to an alternative view in contrast to serial stages of mental processing, which has emerged from growing insights of the way in which perception, cognition, and

action would interrelate in an actual brain. For instance, neurophysiological studies often observe cortical areas traditionally thought as "perceptual" or "motor" in nature to contain signals appropriate for higher-order "cognitive" decision-making (Gold & Shadlen, 2007; Schall, 2005; Tosoni, Galati, Romani, & Corbetta, 2008), implying a blending and continuous flow between the neural subsystems mediating perception, cognition, and action. This, and much other evidence, has led to the view that tentative results from ongoing processing of the perceptual system continuously update the cognitive system, whose ongoing results continuously update the motor system, producing a continuous, cascadic flow of mental processing (e.g., Cisek, 2007; Rogers & McClelland, 2004; Spivey, 2007; Spivey & Dale, 2004). In the context of person perception, a dynamic continuity account argues that tentative, ongoing information extracted from another's face continuously updates semantic representations[1] of that information (e.g., "he's [tentatively] male"), whose ongoing updates are immediately and continuously shared with the motor system to guide action over time (Freeman, Ambady, Rule, & Johnson, 2008). Thus, in this view, an individual may begin preparing to act on partially processed information extracted from another's face before the perceptual and cognitive systems have completely finished seeing and interpreting what had been presented.[2]

How might this hypothesized continuous flow between person perception and action be accomplished at a neural level? Consider a task where participants must make a bodily movement based on the perception of a face's sex—for instance, a left-hand movement indicating male and a right-hand movement

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[1]A face's sex-category, as outlined in Bruce and Young's (1986) classic model of face perception, is a type of "visually-derived semantic information." Other types of semantic representation triggered by faces would be race-category or emotion-category, among others.

[2]Although it is proposed that an ongoing cascade of information continuously passes between the neural subsystems for perception, cognition, and action, some shifts in mental processing can manifest extremely rapidly and nonlinearly so that they begin to approximate discrete-like transitions at some levels of analysis (e.g., "phase transitions"; beim Graben, 2004; Dale & Spivey, 2005; Spivey, Anderson, & Dale, 2009). Regardless, however, a genuine discontinuity in the system would be extremely unlikely. That said, because at some coarser levels of analysis shifts in mental processing may exhibit rapid nonlinearities that approximate discrete-like transitions, approaches emphasizing serial processing and discrete–symbolic representations may be valuable in some contexts. Moreover, such approaches are not necessarily irreconcilable with dynamic approaches emphasizing parallel–continuous processing and distributed representations (Dale, Dietrich, & Chemero, 2009).

indicating female. One possibility is that perceptual processing of another's face in the occipito-temporal cortex (for sex-category, e.g., in the lateral fusiform gyrus; Freeman, Rule, Adams, & Ambady, 2010) continuously sends off ongoing results of processing into higher-order integrative regions such as the prefrontal cortex (Kim & Shadlen, 1999), in addition to regions involved in decision-making and action selection, such as the basal ganglia (Bogacz & Gurney, 2007) and the motor cortices (Cisek & Kalaska, 2005). In doing so, face perceptual processing provides tentative support for response alternatives (e.g., some facial cues provide 75% support for the male category and other facial cues provide 25% support for the female category; Freeman et al., 2008). The basal ganglia and higher-order regions such as the prefrontal cortex force these partially active representations (e.g., 75% male, 25% female) to compete, and the ongoing results of this competition are fed back to lower-level cortices where visual specification is more precise and results can be verified (Bouvier & Treisman, 2010; Treisman, 1996). Lower-level regions then update higher-order regions by sending back revised information (e.g., 85% male, 15% female). Across cycles of processing, ongoing results of this competition continuously arrive in the motor cortices, while the motor cortices prepare tentative motor plans accordingly (Cisek, 2007).

Indeed, neurophysiological work shows that the monkey motor cortex hosts multiple potential motor plans simultaneously (e.g., *both* a left- and a right-hand movement), while one becomes gradually more active (leading to an actual movement), whereas the other is gradually suppressed, as information accumulates over time (Cisek & Kalaska, 2005). During this motor cortex competition between potential actions (e.g., 85% left hand, 15% right hand), which is continuously updated by competitive face processing (e.g., 85% male, 15% female), a stable interpretation is eventually settled on (e.g., ~100% male, ~0% female), resulting in a final selected action that is then executed (e.g., a left-hand movement indicating male). Such an account of the person perception–action link would be consistent with several recent neurobiological decision-making models and backed by a great number of neuronal recordings in nonhuman primates (Cisek, 2007; Cisek & Kalaska, 2005; Glimcher, 2001; Kim & Shadlen, 1999; Rogers & McClelland, 2004; Rolls & Tovee, 1995; Smith & Ratcliff, 2004; Spivey, 2007; Usher & McClelland, 2003). In the present research, we test a proposal at the core of this account—that ongoing results from the perceptual-cognitive processing of

another's face continuously flow into the motor cortex to prepare for action over time.

Recent work has provided indirect behavioral evidence suggesting this possibility. For instance, in tasks during which computer mouse movements are recorded en route to responses on the screen, several studies have suggested that the perceptual–cognitive processing of social stimuli is reflected in actions of the hand (Freeman & Ambady, 2009; Freeman et al., 2008; Freeman, Pauker, Apfelbaum, & Ambady, 2010b; Wojnowicz, Ferguson, Dale, & Spivey, 2009). Although such mouse-tracking studies suggest that results from person perception may continuously interact with the motor system, they cannot directly separate out perceptual–cognitive processing from motor processing. A methodology that *is* capable of doing this, which would also extend this prior mouse-tracking work by shedding light on underlying neural dynamics, is event-related brain potentials (ERPs). Here, across two studies, we investigate the relationship between person perception and action by examining the electrophysiological activity of the human brain. Using this activity, we explore how the perception of an aspect of another's face leads into to the motoric reaction to that perception. We focus on the perception of sex-category and the production of a hand movement based on that category, because, given prior work (Freeman & Ambady, 2009; Freeman et al., 2008), we reasoned that a typical/atypical manipulation with sex-category could reliably reveal the time-course of its semantic processing—a feature required by the present research.

Across two studies, we test the proposal that ongoing processing of another's face continuously cascades into action. In Study 1, we tease apart neural activity associated with perceptual–cognitive (semantic) processing of a face's sex-category (using N300/N400 components) and neural activity associated with preparing for action based on that sex-category (using the lateralized readiness potential, LRP, component). How these components index the semantic processing of a face's category information and action preparation based on that, respectively, are detailed later. If tentative, ongoing semantic processing of a face's sex-category gradually builds into action, the LRP should begin activating while N300/N400 effects are still evolving in parallel. If not, the LRP should begin activating only after N300/N400 effects have completed. In Study 2, we test whether the processing of one facial cue can partially activate the motor system to prepare for action before perceptual analysis of the face has been completed. This would be direct evidence that partial results from face processing can

continuously flow into the motor system before face perception has finalized.

STUDY 1

To examine neural activity associated with the semantic processing of a face's sex-category, we used atypical exemplars, a notion widely exploited in the cognitive categorization and psycholinguistics literatures (Dale, Kehoe, & Spivey, 2007; Murphy, 2002; Rosch, 1978). For instance, an important question in psycholinguistics is how semantic knowledge is extracted from a word or object. In person perception research, we have a very similar interest: How is semantic knowledge (e.g., sex-category) extracted from a face? One useful technique psycholinguists have used is to challenge the language system by a word that is anomalous or conflicting with the semantic context. For instance, the phrase "all dogs are instruments" is strange for readers because "instruments" is not a word typically used to describe "dogs." Thus, when participants arrive at the word "instruments" in the sentence, the semantic knowledge extracted from it requires a great deal of processing to integrate it with the words that preceded it (in order to comprehend the sentence). Because semantically challenging words require more semantic processing to resolve them, researchers can exploit these words to understand the dynamics of semantic processing more broadly.

Previous ERP studies have consistently found that a negative potential emerges approximately 400 ms after a semantic anomaly is presented ("instruments" in the sentence above), denoted as the N400 (Holcomb, 1993; Kutas & Hillyard, 1980). The N400 is also larger for words preceded by semantically unrelated primes (e.g., "cat" preceded by "car") relative to words preceded by related primes (e.g., "cat" preceded by "dog"). Using image stimuli rather than word stimuli, studies have additionally found an N300 effect with a different spatial topography co-occurring with the slightly later N400. When images are preceded by unrelated primes (e.g., a cat picture preceded by a car picture) rather than related primes (e.g., a cat picture preceded by a dog picture), a frontally distributed negativity arises around 200–300 ms, which is then followed by a central–parietal negativity between 300 and 500 ms (Barrett & Rugg, 1990; McPherson & Holcomb, 1999). Importantly, the N300 and N400 potentials are not modulated by low-level visual or auditory information, are elicited by stimuli in multiple sensory modalities, and are highly sensitive to semantic manipulations, such as those described above, solidifying the idea that these

potentials reflect integrative, higher-order semantic processing (for review, see Lau, Phillips, & Poeppel, 2008).

The semantic processing indexed by the N400 and N300 potentials is also involved in categorization. When presented with a series of words belonging to the same semantic category, a subsequent word elicits an N400 if it is a nonmember of that category (Polich, 1985). Moreover, when presented with sentences such as "a poodle is a dog," an N400 is elicited if the exemplar is a nonmember of the category, regardless of whether the sentence is true or false (Kounios & Holcomb, 1992). The N400 is sensitive not only to category membership, but also to its typicality. When one is given pairs of category and exemplar words (e.g., "dog" followed by "poodle"), the exemplar word elicits an N400 not only when it is a nonmember of the category but also when it is an atypical member (e.g., "bird" followed by "penguin"; Fujihara, Nageishi, Koyama, & Nakajima, 1998; Heinze, Muente, & Kutas, 1998). Together, these findings suggest that the N400 reflects the semantic processing required to match an exemplar ("poodle") with a corresponding category ("dog"). When categorization is particularly difficult, as with nonmembers or atypical exemplars, semantic processing is more heavily recruited, and this is indexed by the N400.

Given the N300's and N400's role in categorization, one way to investigate the ERP correlates of extracting a face's sex-category would be to ask participants to categorize the sex of sex-typical and sex-atypical faces and inspect semantic effects such as the N300 and N400 potentials. Just as categorizing an atypical exemplar word requires additional semantic processing, indexed by the N400, so too should this additional semantic processing be required for placing a sex-atypical face into a given sex-category. Indeed, although the N400 is most often associated with linguistic processes, several studies have reported N300/N400 effects using face stimuli as well (e.g., Barrett & Rugg, 1989; Barrett, Rugg, & Perrett, 1988; Wiese, Schweinberger, & Neumann, 2008). Thus, in social categorization, N300/N400 potentials should provide an index of the time-course of extracting social category knowledge from faces.

The LRP serves a real-time neural index of motor preparation. In most LRP studies, one response is executed by the left hand and the other response by the right hand. Because primary motor cortices in either hemisphere prepare movements of the contralateral hand, left-hand responses are governed by right motor cortex (measured by the C4 electrode) and right-hand responses are governed by left motor cortex (measured by the C3 electrode). Often several hundred

milliseconds prior to execution of a hand movement, ERP waveforms at C3 and C4 sites begin to lateralize, with more negative amplitudes at the contralateral site. For instance, preceding a left-hand movement, waveforms at the C4 site (over right motor cortex) are more negative-going than those at the C3 site (over left motor cortex). This reflects preferential motor activation for the to-be-executed hand. Moreover, because the LRP is derived using a double subtraction procedure (detailed below), it serves as a pure measure of motor preparation, with minimal influence from sensory input or other confounding factors (Eimer, 1998). Typically emerging hundreds of milliseconds prior to motor execution, the LRP can be interpreted to reflect the accumulating results from perceptual–cognitive processing that are cascading into the motor cortex for the preparation of a hand response (Eimer, 1998; Miller & Hackley, 1992).

By examining N300/N400 and LRP effects in a sex categorization task using a typical/atypical manipulation, we can tease apart two neural processes: the semantic processing of a face's sex-category and the motor preparation of a hand movement based on that sex-category. As described above, one possibility is that face perception must finalize before correctly extracted information is sent on to the motor system, consistent with traditional cognitive theories. Another possibility, consistent with a dynamic continuity account, is that motor preparation of the hand associated with a face's correct sex-category would unfold in parallel with the semantic processing of that sex-category. Specifically, we hypothesize that sex-atypical faces will elicit more negative N300/N400 potentials relative to sex-typical faces, providing an index of the semantic processing involved in extracting sex-category from the face. Critically, we also assess the LRP to determine whether the motor cortex receives correct information about a face's sex-category while processing of that sex-category is still ongoing or whether it begins only after processing has finalized.[3]

Method

Participants

Twenty-three healthy, right-handed volunteers participated in exchange for $20 each.

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[3]Analysis of the data from Study 1 targeting different components (the N170 and P1) at earlier epochs (between 100 and 190 ms) is reported elsewhere (Freeman, Ambady, & Holcomb, 2010a). That study focused on basic visual encoding of sex-category facial content.

Stimuli

To conduct morphing along sex, we used 3-D face modeling software, FaceGen Modeler 3.1 (Singular Inversions, Vancouver, Canada), enabling the semirandomized generation of face stimuli with a high level of realism. This software allowed for sexually dimorphic face information to be manipulated along a continuum of sex (as based on anthropometric parameters of the human population) while unconfounding all other perceptual information. Fifty unique male faces were generated at the anthropometric male mean, and 50 unique female faces were generated at the anthropometric female mean, together composing the typical condition. The 50 typical male faces were then morphed approximately 25% toward the female mean, and the 50 typical female faces were then morphed approximately 25% toward the male mean, together composing the atypical condition. Faces were directly oriented and cropped so as to preserve only the internal face (see Figure 1 for sample stimuli).

This morphing technique also allowed us to eliminate low-level visual differences (e.g., brightness, intensity) that might have covaried with the typical vs. atypical conditions. This is because morphing a male to be more atypical and morphing a female to be more atypical have exactly opposing effects in terms of low-level visual information. For instance, male faces are, on average, darker than female faces, which was reflected in our morphing algorithm (Blanz & Vetter, 1999). Therefore, when a male face was made more atypical, it became slightly lighter; when a female face was made more atypical, it became slightly darker. Because the typical and atypical conditions each contained both male and female faces, these opposing effects canceled each other out. As such, the typical and atypical conditions were tightly controlled against extraneous low-level visual-evoked responses.

Behavioral procedure

Face stimuli were presented in a pseudorandomized order on a black background using a computer monitor directly in front of participants. Participants were instructed to categorize faces by sex as quickly and accurately as possible using left- vs. right-hand button presses (whether male/female was left/right was counterbalanced). Participants were also told to avoid blinking during the trial and to only blink when a message appeared instructing them to do so. At the beginning of each trial, a fixation cross was presented for 800 ms, followed by a 500 ms interstimulus interval (ISI) of a blank screen. Next, the face appeared for 600 ms, followed by a 1000 ms ISI. Finally, a message
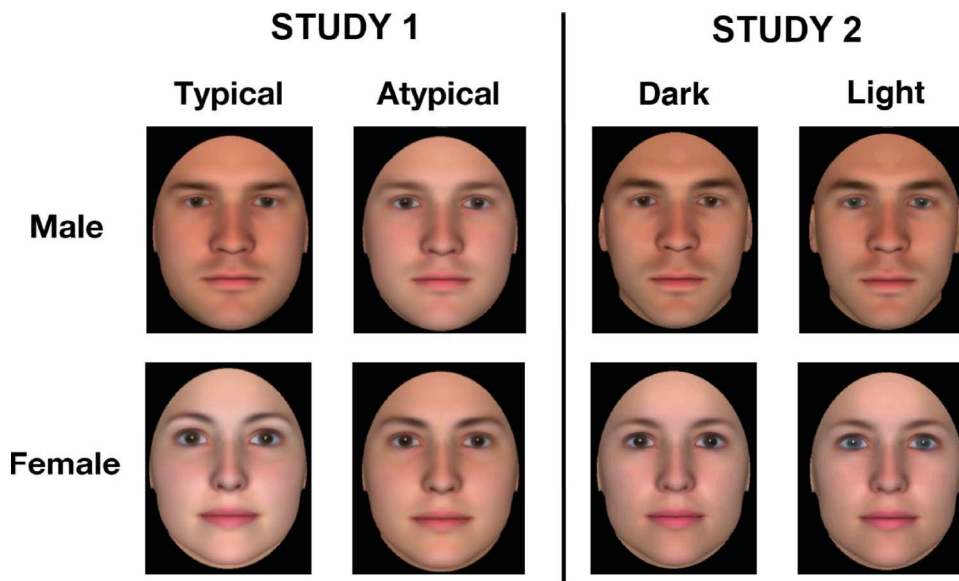
Figure 1. Sample stimuli. In Study 1, typicality of target sex was manipulated by morphing sexually dimorphic information of the internal face. In Study 2, eye color was manipulated to be either dark or light.

informing participants to blink appeared for 2000 ms. After a 300 ms ISI, the next trial began. Participants completed several practice trials prior to experimental trials.

EEG acquisition

Participants were seated in a comfortable chair in a sound-attenuated darkened room. An electro-cap with tin electrodes was used to record continuous EEG from 29 sites on the scalp, including sites over left and right fronto-polar (FP1/FP2), frontal (F3/F4, F7/F8), frontal–central (FC1/FC2, FC5/FC6), central (C3/C4), temporal (T5/T6, T3/T4), central–parietal (CP1/CP2, CP5/CP6), parietal (P3/P4), and occipital (O1/O2) areas and five midline sites over the frontal pole (FPz), frontal (Fz), central (Cz), parietal (Pz), and occipital (Oz) areas. In addition, five electrodes were attached to the face and neck area: one below the left eye (to monitor for vertical eye movement and blinks), one to the right of the right eye (to monitor horizontal eye movements), one over the left mastoid (reference), one over the right mastoid (recorded actively to monitor for differential mastoid activity), and one on the nose. All EEG electrode impedances were maintained below 5 kΩ (for scalp electrodes), 10 kΩ for eye and nose electrodes, and 2 kΩ for mastoid electrodes. The EEG was amplified by an SA Bioamplifier with a bandpass of 0.01 and 40 Hz and the EEG was continuously sampled at a rate of 250 Hz.

Data analysis

Averaged ERPs were calculated offline from trials free of ocular and muscular artifact. ERPs were generated by time-locking to the onset of face stimuli. To determine N300 and N400 effects, we calculated mean amplitude values, relative to a 100 ms prestimulus baseline, for the voltage points between post-stimulus time windows of 250–350 ms (N300) and 350–550 ms (N400). These amplitude values were then submitted to repeated-measures analyses of variance (ANOVAs) having two levels of *typicality* (typical and atypical). To capture neural activity in parasagittal columns of scalp electrodes along the anterior–posterior axis of the head (Figure 2), four separate ANOVAs were conducted. A midline analysis contained five levels of *electrode site* (FPz, Fz, Cz, Pz, Oz). A medial analysis contained three levels of *electrode site* and two levels of *hemisphere* (FC1/FC2, C3/C4, P1/CP2). A lateral analysis contained four levels of *electrode site* and two levels of *hemisphere* (F3/F4, FC5/FC6, CP5/CP6, P3/P4). Finally, a peripheral analysis contained five levels of *electrode site* and two levels of *hemisphere* (FP1/FP2, F7/F8, T3/T4, T5/T6, O1/O2). When appropriate, Geisser-Greenhouse corrections were applied. For simplicity, only effects involving *typicality* are reported.

To generate LRP waveforms for the typical and atypical conditions, average waveforms at C3 and C4 electrode sites underwent a double subtraction procedure (Eimer, 1998). For each condition, we computed
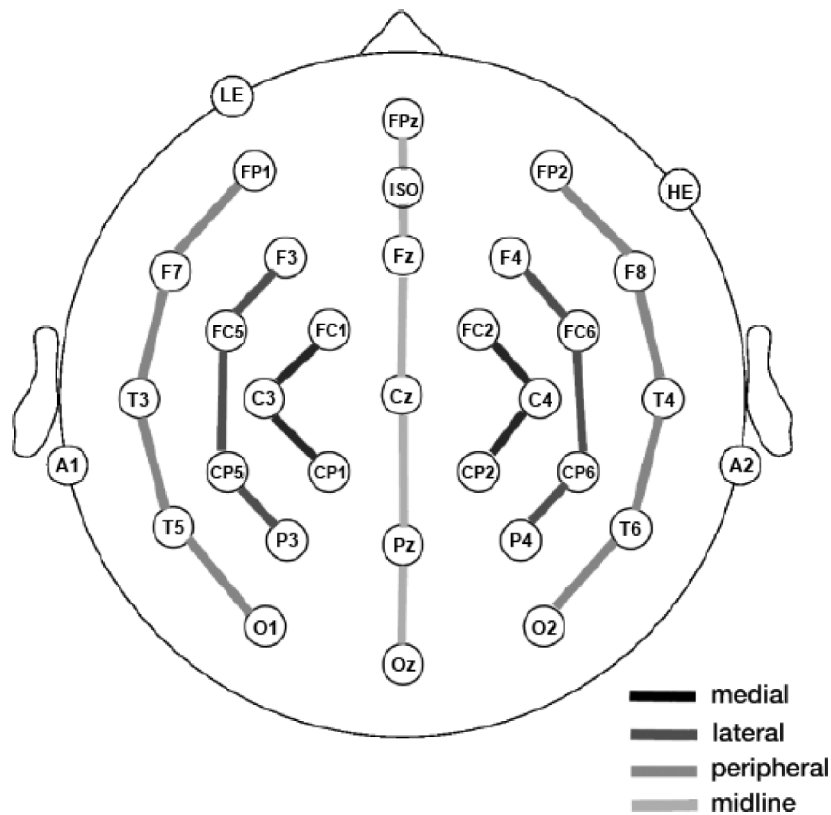
Figure 2.   Diagram of the electrode montage used in Studies 1 and 2.

the difference between contralateral and ipsilateral activity by generating one difference waveform (C3 – C4) for trials involving right-hand responses and another difference waveform (C3 – C4) for trials involving left-hand responses. These two difference waveforms were then subtracted from one another, $(C3 - C4)_{left} - (C3 - C4)_{right}$, to form the LRP. See Eimer (1998) for further details on this double subtraction procedure. We calculated mean amplitude (relative to 100 ms prestimulus baseline) for LRP voltage points between a poststimulus time window of 250–700 ms. Mean amplitudes for the typical and atypical conditions were submitted to a paired-samples t-test.

In the present study and Study 2, all t-tests are two-tailed except those with a directional *a priori* hypothesis.

Results

Trials in which sex was categorized incorrectly (4.2%) were discarded. Expectedly, participants were significantly quicker to categorize the sex of typical targets ($M = 573$ ms, $SE = 22$ ms) than atypical targets ($M = 592$ ms, $SE = 25$ ms), $t(22) = 2.61, p < .05$.

Grand-average waveforms at all scalp electrode sites, time-locked to the onset of face stimuli, appear in Figure 3. At approximately 250 ms poststimulus, waveforms for atypical targets began showing a robust negativity effect. This was distributed widely across electrode sites over temporal, parietal, and occipital cortices. This is best illustrated in Figure 4, which depicts voltage maps across the scalp between face onset (0 ms) and 600 ms thereafter. Note the emergence of a frontally distributed negativity around 250 ms, which then travels posterior and dissipates by approximately 600 ms. To assess this effect statistically, we compared the mean amplitude of waveforms for the typical vs. atypical conditions between a 250–350 ms time window (the N300) and a 350–550 ms window (the N400).

N300

Between 250 and 350 ms, atypical targets elicited more negative ERPs than typical targets (main effects of *typicality*) across all four parasagittal columns: midline, $F(1, 22) = 66.91, p < .0001$, medial, $F(1, 22) = 212.66, p < .0001$, lateral, $F(1, 22) = 4.88, p < .05$, and peripheral, $F(1, 22) = 12.20, p < .01$. ANOVAs
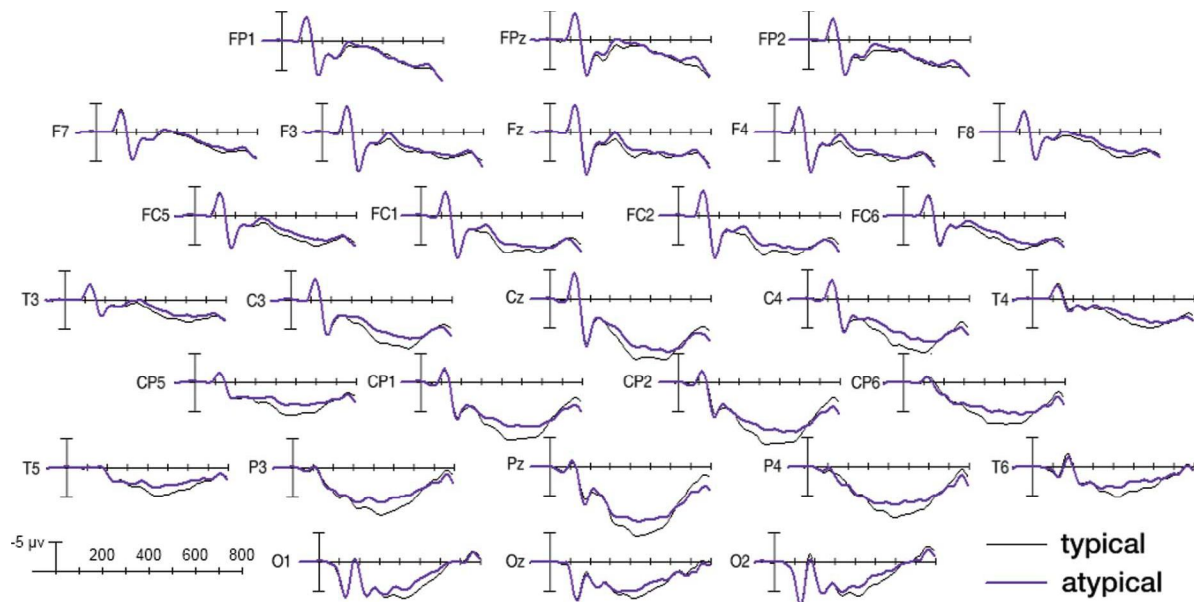
Figure 3. Grand-average waveforms for typical and atypical faces of Study 1. Negative is plotted up. Top of the figure corresponds with anterior aspect of the head, as depicted in Figure 2. Note the higher negativity for atypical faces (relative to typical faces) emerging around 250 ms at anterior sites and around 350 ms at posterior sites. These denote the N300 and N400.

also elicited significant *typicality × electrode site* interactions: midline, $F(4, 88) = 4.85$, $p = .01$, medial, $F(2, 44) = 55.23$, $p < .0001$, and peripheral, $F(4, 88) = 5.75$, $p < .01$, but not in the lateral column, $F(3, 66) = 1.02$, $p = .37$. The three columns with a factor of *hemisphere* also revealed *typicality × hemisphere* interactions: medial, $F(1, 22) = 77.74$, $p < .0001$, lateral, $F(1, 22) = 329.70$, $p < .0001$, and peripheral, $F(1, 22) = 31.26$, $p < .0001$, and *typicality × electrode site × hemisphere* interactions: medial, $F(2, 44) = 41.13$, $p < .0001$, lateral, $F(3, 66) = 9.83$, $p < .001$, and peripheral, $F(4, 88) = 2.81$, $p = .05$. Visual inspection of the voltage maps in Figure 4 indicate (and planned comparisons confirmed) that these interaction effects

arose because the N300 negativity had a centro-frontal distribution, starting initially in frontal sites and progressively moving more posterior, with a slight lateralization to the right hemisphere.

N400

Between 350 and 550 ms, atypical targets elicited more negative ERPs than typical targets (main effects of *typicality*) across all four parasagittal columns: midline, $F(1, 22) = 157.37$, $p < .0001$, medial, $F(1, 22) = 294.09$, $p < .0001$, lateral, $F(1, 22) = 183.54$, $p < .0001$, and peripheral, $F(1, 22) = 91.64$, $p < .0001$. These main effects were qualified by significant *typicality*
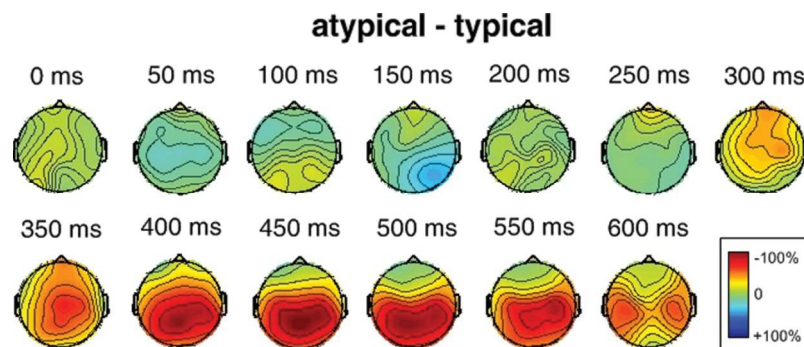
Figure 4. Voltage maps of normalized difference waves, atypical – typical, depicting differences in neural potentials to typical vs. atypical faces. Top of each figure corresponds with anterior aspect of the head, as depicted in Figure 2. A negativity effect emerges around 250 at anterior sites, which then gradually moves more posterior into a strong centro-posterior negativity effect. This reflects the evolution of enlarged N300 and N400 effects in response to atypical faces.

× *electrode site* interactions: midline, $F(4, 88) = 7.07$, $p < .01$, medial, $F(2, 44) = 47.12$, $p < .0001$, and peripheral, $F(4, 88) = 12.98$, $p < .0001$, but not in the lateral column, $F(3, 66) = 1.45$, $p = .25$. The three columns with a factor of *hemisphere* also revealed *typicality × hemisphere* interactions: medial, $F(1, 22) = 84.54$, $p < .0001$, lateral, $F(1, 22) = 9.96$, $p < .01$, and peripheral, $F(1, 22) = 39.79$, $p < .0001$. There was a *typicality × electrode site × hemisphere* interaction in the medial column, $F(2, 44) = 54.88$, $p < .0001$, a marginally significant interaction in the peripheral column, $F(4, 88) = 2.30$, $p = .08$, but a nonsignificant interaction in the lateral column, $F(3, 66) = .591$, $p = .58$. Visual inspection of the voltage maps in Figure 4 indicate (and planned comparisons confirmed) that these interaction effects arose because this N400 effect was distributed at central and posterior sites, with a slight lateralization to the right hemisphere.

Stimulus-locked LRP

The grand average LRP waveforms for the typical and atypical conditions appear in Figure 5. The LRP for typical faces emerged at approximately 300 ms as a positive-going deflection (Figure 5). Between 250 and 700 ms, this LRP wave was reliably more positive than baseline, one-sample, $t(22) = 4.96$, $p < .0001$. Note that the LRP for atypical faces had a slightly later onset than the LRP for typical faces and, more importantly, became larger than the LRP for typical faces by approximately 400 ms, and this increased positivity persisted throughout its course. Between 250 and 700 ms, the LRP for atypical faces showed reliably more positive activity than baseline, one-sample, $t(22) = 7.59$, $p < .0001$. Within this epoch, the LRP for atypical faces was also significantly larger than the LRP for typical faces, $t(22) = 2.93$, $p < .01$. These LRP effects were significantly more positive than baseline as early as 300–350 ms: typical faces,

Figure 5. Grand-average LRPs for typical and atypical faces of Study 1. The LRP for atypical faces grows larger in size than the LRP for typical faces, indicating greater competition between the motor cortices.

one-sample, $t(22) = 6.28$, $p < .0001$ and atypical faces, one-sample, $t(22) = 3.87$, $p < .001$.

Discussion

Relative to typical faces, ERPs for atypical faces were more negative between 250 and 350 ms and between 350 and 550 ms. The frontal distribution of the 250–350 ms negativity and more posterior distribution of the 350–550 ms negativity suggest that these effects were part of the N300 and N400 family, as is characteristically seen in the semantic priming of image stimuli (e.g., McPherson & Holcomb, 1999). Although the N400 is a component most often associated with linguistic processes, several studies have reported N300 and N400 effects using face stimuli (e.g., Barrett & Rugg, 1989; Barrett et al., 1988). Using pairs of sequential faces, N300 and N400 effects were elicited by faces that did not match the preceding identity (Barrett et al., 1988) or were not of the same occupational category (Barrett & Rugg, 1989). In a repetition priming study, the N300 and N400 were attenuated by faces that had not been previously encoded (Wiese et al., 2008). In these studies, knowledge of a target's identity or occupation served as a semantic context; when a subsequent face violated this context, N300 and N400 effects arose. Interestingly, in the present study, perceivers were given no explicit semantic context. Rather, when gendered facial cues were difficult to integrate into the implicit context of a sex categorization, N300 and N400 amplitudes increased (see Holcomb, 1993, for discussion of implicit context effects and the N400). Although N300/N400 effects are often associated in tasks where there is an explicit context, many studies also find these effects in tasks with single-item trials that lack any explicit context (e.g., Kounios & Holcomb, 1994), such as that used in the present study. Extending from a large psycholinguistics literature (Lau et al., 2008), we interpret the typical/atypical N300/N400 modulation to reflect the semantic processing required to integrate accumulating knowledge of gendered face information into a coherent sex categorization.

Concerning the LRP, both typical and atypical faces elicited LRPs that were significantly more positive than baseline between 250 and 700 ms and these were reliable as early as 300–350 ms. Moreover, the LRP for atypical faces grew larger than the LRP for typical faces between 250 and 700 ms. Figure 5 indicates that, in spite of its slightly later onset (consistent with the reaction time data), the LRP for atypical faces became larger than the LRP for typical faces by
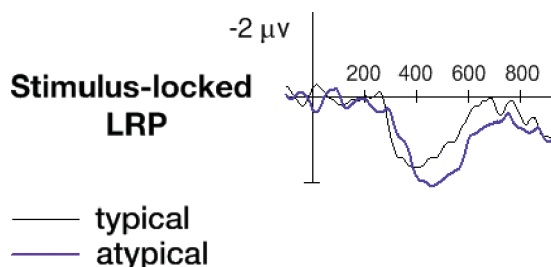
approximately 400 ms, and this increased amplitude continued over time. This suggests that atypical faces elicited more motor response competition (due to the parallel activation of male and female category representations), as has been shown behaviorally in prior work (Freeman & Ambady, 2009; Freeman et al., 2008). A larger LRP amplitude indicates response competition because in cases where two response alternatives are simultaneously competing (one tied to the left hand and the other tied to the right hand), accumulating activation for the correct response at contralateral motor cortex tends to be accompanied by reciprocal inhibition of the incorrect response at ipsilateral motor cortex (Cohen, Servan-Schreiber, & McClelland, 1992; Praamstra & Seiss, 2005; Vidal, Grapperon, Bonnet, & Hasbroucq, 2003). Thus, for stimuli that trigger more response competition (relative to less), contralateral motor activity tends to become more negative (activated) and ipsilateral motor activity tends to become more positive (inhibited). Due to the double subtraction procedure that derives the LRP, such a pattern of contralateral activation and ipsilateral inhibition, induced by response competition, would lead to larger LRP amplitudes. This is consistent with prior work (e.g., De Jong, Coles, Logan, & Gratton, 1990; Seifert, Naumann, Hewig, Hagemann, & Bartussek, 2006).

Lastly, and most importantly, the N300/N400 and LRP dynamics were concurrent. By approximately 250 ms, sex-category knowledge was being processed, as indicated by the more negative N300 potential for sex-atypical faces. This semantic processing continued through at least 550 ms. As for the LRPs, they began to emerge by approximately 300 ms (while semantic processing was still ongoing) and these continued until motor execution (mean reaction times: 573 ms for typical faces and 592 ms for atypical faces). Motor response preparation, as indicated by the LRP, was continuously evolving in parallel with accruing sex-category knowledge, as indicated by the N300/N400 effects. It appears that as social category knowledge becomes gradually more available, tentatively available semantic results are continuously transmitted into the motor cortex to prepare action. If this were not the case, the LRP would not be able to lateralize until after the N300/N400 effects had finished.

It is possible that a serial stage-based account could potentially reconcile our finding of substantial temporal overlap between N300/N400 and LRP effects. For instance, perhaps at a moment following face presentation, a critical amount of semantic sex-category processing had finalized (e.g., 90% confident decision that the face is male), and this decision was then discretely transmitted to the motor cortex.

The motor cortex could then prepare the movement based on that decision, which had completely arrived in the motor cortex before motor preparation had begun. However, there are two reasons why this is unlikely. First, N300/N400 effects had persisted all the way to actual motor execution, indicating that semantically resolving a face's sex-category was ongoing up until the moment participants made a hand movement. Moreover, we found evidence suggesting that sex-atypical faces elicited greater motor response competition (stronger activation of contralateral motor cortex and inhibition of ipsilateral motor cortex). This indicates that the ongoing competition between male and female categories involved in extracting a face's sex (which would be exacerbated for sex-atypical targets; Freeman et al., 2008) was reaching the motor cortices. That is, if a finalized decision discretely arrived in the motor cortices in serial fashion, then the motor cortices should not host any competition between tentative responses (as a sex-category decision was already finalized). However, if ongoing perceptual–cognitive processing of another's face continuously updates the motor system, as we predict, then the motor cortices should indeed show stronger competition between left and right hand movements for sex-atypical faces because the stronger perceptual–cognitive competition between sex-categories would be reflected in the motor system as well.

Another possibility is that the temporal overlap between N300/N400 and LRP effects was spuriously produced by averaging across individual trials that each contained a discrete transition between the N300/N400 and LRP effects, but that the onset of this transition varied in time on a trial-by-trial basis. In principle, each individual trial may have involved the completion of perceptual–cognitive processing that then sent a discrete command to the motor cortex, but because this transition occurred at varying onsets across trials, an average effect of temporal overlap was produced. However, although this situation could produce overlap in the N300/N400 and LRP time-courses, it cannot account for the finding that sex-category competition cascaded into a competition between the motor cortices (greater LRP amplitude for sex-atypical targets). If perceptual–cognitive processing finalized prior to motor preparation, no greater motor competition should be seen for sex-atypical relative to sex-typical faces. Thus, a more parsimonious account is that that ongoing updates of semantic processing of another's face are continuously cascaded into the motor system, as predicted by a dynamic continuity account of person perception. In Study 2, we examine this continuous transmission more closely.

STUDY 2

We test whether information about the perceptual processing of one facial cue, eye color, can be transmitted to the motor system before perceptual analysis of the face has completed. This would be more evidence for the transmission of partial products of face perceptual processing into the motor system across the process of social categorization.

We combined a dual-choice categorization task with a go/no-go paradigm, as done in similar work using ERP measures as evidence for partial transmission (Miller & Hackley, 1992). Participants were asked to categorize the eye color of a face using a left or right hand response, but only to do this for one sex (go trials) and withhold a response for the other sex (no-go trials). Thus, every trial involved two independent perceptual extractions: eye color and sex. Eye color was chosen because it is not sexually dimorphic and its perception is independent from the processing of sex. It was also chosen because we reasoned that eye color should be extracted more rapidly than sex, as it is a simpler perceptual variable (blue/green vs. brown). Access to eye color information should be available earlier than access to a target's sex-category membership. Thus, these two cues give us the opportunity to test whether information about one facial feature can be partially transmitted into the motor cortex before face perception has been finalized.

Participants engaged in two tasks: *go-male/no-go-female* (where participants categorize eye color only for men) and *go-female/no-go-male* (where participants categorize eye color only for women). On go-trials, we can expect that a reliable LRP will develop that precedes participants' eye color categorizations. More critically, however, on no-go trials, two possibilities could occur. The first would be that, because participants were instructed to not go on these trials and did not execute a response, no LRP would develop. This would be consistent with classic theorizing, such that face perception must be finalized before information is sent onto the motor system. However, we predict that a partial LRP would develop, where information about eye color partially prepares contralateral motor cortex to make a response even though no response is actually executed. This partial LRP, which has been found in previous work (e.g., Miller & Hackley, 1992), would be considerably smaller and shorter in duration than LRPs found for go-trials, but nonetheless significant. This would be evidence suggesting that products of face perceptual processing can be partially transmitted into subsequent processing stages as the information becomes available, rather than when perceptual analysis of the face has been finalized.

Method

Participants

Twenty healthy, right-handed volunteers participated in exchange for $20 each.

Stimuli

Face stimuli were created using the same software and were presented in an identical manner as in Study 1. For the *go-male/no-go-female* task, 60 unique male faces were generated at the anthropometric male mean, half of which were light-eyed and half of which were dark-eyed, and 60 unique male faces were generated at the anthropometric female mean, half light-eyed and half dark-eyed. See Figure 1 for sample stimuli. To encourage motor response preparation for *no-go* female faces, we ensured female faces were presented more rarely than male faces by using an additional 100 male faces as fillers (Miller & Hackley, 1992). For the *go-female/no-go-male* task, a separate set of 60 unique female faces, half light-eyed and half dark-eyed, and 60 unique male faces, half light-eyed and half dark-eyed, were generated. An additional 100 female faces were used as fillers to encourage *no-go* response preparation.

Behavioral procedure

Whether participants completed the *go-male/no-go-female* or *go-female/no-go-male* task, first vs. second was counterbalanced across participants. In each task, face stimuli were presented in a pseudorandomized order on a black background using a computer monitor directly in front of participants. For the *go-male/no-go-female* task, participants were instructed to indicate the eye color (light or dark) of only male faces (and not female faces) as quickly and accurately as possible using left- vs. right-hand button presses. For the *go-female/no-go-male* task, they were instructed to indicate the eye color of only female faces (and not male faces). For both tasks, whether light/dark was left/right was counterbalanced. Participants were also told to avoid blinking during the trial and to only blink when a message appeared instructing them to do so. At the beginning of each trial, a fixation cross was presented for 800 ms, followed by a 500 ms ISI of a blank screen. Next, the face appeared for 600 ms, followed by a 1000 ms ISI. Finally, a message informing participants to blink appeared for 2000 ms. After a 300 ms ISI, the next trial began. Participants completed several practice trials prior to experimental trials.

EEG acquisition

Acquisition parameters were identical to those in Study 1.

Data analysis

Artifact rejection, averaging, and stimulus time-locking were done using identical procedures of Study 1. LRP waveforms for go and no-go trials were calculated using the double subtraction procedure outlined in Study 1. Because we hypothesized a partial LRP on no-go trials that would be small in amplitude and short in duration, we inspected LRP effects in increments of small time windows. We calculated mean amplitude of LRP voltage points (relative to a 100 ms prestimulus baseline) between 300 and 400 ms, 400 and 500 ms, and 500 and 600 ms.

Results

No-go trials that elicited an accidental response (2.8%), go-trials that did not elicit any response (2.0%), and go-trials in which eye color was categorized erroneously (4.1%) were discarded from behavioral and ERP analysis. The mean reaction time for categorizations was 692 ms ($SE = 30$ ms).

Stimulus-locked LRP

The grand average LRP waveforms for go and no-go trials appear in Figure 6. The LRP for go trials emerged at approximately 400 ms (Figure 6). This was reliably more positive than baseline between 300 and 400 ms, one-sample, $t(19) = 2.21$, $p < .05$, 400–500 ms, one-sample, $t(19) = 3.71$, $p = .001$, and 500–600 ms, one-sample, $t(19) = 3.86$, $p = .001$. Although more difficult to see in Figure 6 given its small amplitude, the LRP for no-go trials did appear to gain slight positivity around 400 ms as well, departing from baseline. This no-go LRP was not significantly more positive than baseline between 300 and 400 ms, one-sample, $t(19) = 1.62$, $p = .12$, but reached significance between 400 and 500 ms, one-sample, $t(19) = 2.14$, $p < .05$. This then returned to non-significance by 500–600 ms, one-sample, $t(19) = 1.68$, $p = .11$. Thus, as predicted, no-go trials elicited a partial LRP that was significant between 400 and 500 ms, indicating that perceptual processing partially prepared motor cortex to make a response before face perception had been finalized. This partial preparation emerged at 400–500 ms and decayed by 500–600 ms. Note that no actual hand response was made on these
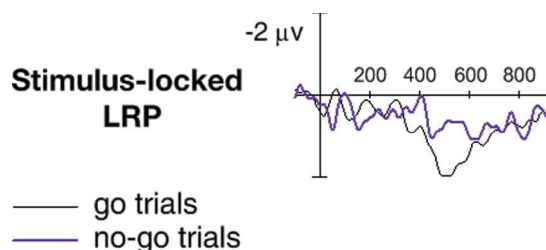

Figure 6. Grand-average LRPs for go and no-go trials of Study 2. Although no hand response was made on no-go trials, a partial LRP was significant between 400–500 ms, although difficult to distinguish here because of its expectedly small amplitude and duration. This reflects partial preparation of a hand response, cued by eye color, before face perception had been finalized.

trials (any no-go trials where a response was accidentally made were excluded). During the 400–500 ms epoch in which the no-go LRP was significant, the LRP for go trials was significantly larger than the LRP for no-go trials, $t(19) = 2.55$, $p < .05$.

Discussion

On go trials, an LRP developed preceding participants' responses. On no-go trials, however, even when participants made no actual hand response, an LRP began to partially develop (for indicating eye color) but then decayed as accumulating knowledge of the target's sex became more available, resulting in the withholding of a response. This partial LRP for no-go trials indicates that perceptual extraction of one facial cue, eye color, led to motor response preparation before perception of sex-category had been finalized. This converges with the finding in Study 1 that the LRP preceding a sex categorization response and the semantic resolution of a target's sex (indexed the N300/N400) were operating in parallel.

Some readers may be concerned by the possibility that the partial motor preparation, evidenced by the partial LRP, was simply a result of a general readiness to make a motor response on every trial regardless of the face presented (since the majority of trials were go, rather than no-go, trials). This is not the case, however, because the LRP does not reflect a general motor preparation, but reflects *correct* motor response preparation (greater activation of contralateral relative to ipsilateral motor cortex). Thus, the partial LRP found here reflected the motor cortex's partial preparation of a hand movement that was correct for a particular face's eye color. The partial LRP, therefore, truly reflected a partial transmission of information about eye color before perception of sex-category had

finalized. The present results, converging with those of Study 1, thus suggest that partial products of perceptual–cognitive face processing are continuously cascaded into the motor system over time.

GENERAL DISCUSSION

Across two studies, brain potentials provided support for the dynamic continuity between person perception and action. Sex-atypical faces (partially appearing like the opposite sex) elicited a frontally distributed negativity between 250 and 350 ms and a more posterior negativity between 350 and 550 ms. The timing and scalp distribution of these negativities indicate that they were modulations of the N300 and N400, respectively. Given a large body of findings in the psycholinguistics literature (for review, Lau et al., 2008), these likely reflect the semantic processing required to integrate accumulating sex-category knowledge into a coherent interpretation of a target's sex. We found that such integrative social category processing, working to bring lower-level visual information into higher-order representations of a target's sex, emerged as early as 250 ms and was in continuous operation up until the moment participants responded (~600 ms). Moreover, while this social category processing was still ongoing, the motor cortex began receiving correct information about a target's sex as early as 300–350 ms, indicated by the onset of preferential activation at contralateral motor cortex in preparation of a correct hand response (the LRP). This is striking. The motor cortex governing a correct hand response was already preparing for action about 300 ms after presentation of a face, which is, on average, about 300 ms before sex categorization responses were made. Thus, the motor cortex already had a tentative (and predominantly correct) interpretation of a target's sex (i.e., the LRP) well before the hand movement was executed, and this interpretation built up continuously over time while social category processing was still ongoing (indexed by the N300/N400 complex). We also found that activation of the motor cortices reflected updates of the perceptual–cognitive competition between sex categories (male vs. female), with stronger sex-category competition for sex-atypical faces (Freeman et al., 2008) triggering more competition between the contralateral vs. ipsilateral motor cortices (left vs. right hand movement). This confirms that ongoing results of sex-category processing were indeed being received by the motor cortices over time (rather than the motor cortices receiving a finalized decision in serial fashion). Thus, motor preparation of the correct hand was continuously being guided in parallel by gradually accumulating sex-category knowledge.

In Study 2, although participants effectively withheld making a hand response for faces of a particular sex (on no-go trials), one facial cue available earlier than sex, eye color, was nevertheless able to partially prepare the motor cortex governing the correct hand (correct—if it were a go rather than no-go trial). This partial preparation then decayed and yielded to the accumulating knowledge of the target's sex. Thus, the results from perceptual processing of one facial cue (eye color) was transmitted into the motor cortex to prepare for action as the perceptual information became available rather than once face perception had been completed. Taken together with the findings of Study 1, the present studies suggest that tentative, ongoing results from perceptual–cognitive face processing are continuously transmitted to motor cortex and that the motor cortex takes those results and simultaneously prepares for action.

These results provide support for the continuous dynamics between person perception and action, and are consistent with growing evidence that the dynamics of action is part and parcel with the dynamics of perception and cognition, such that they continuously change and interact in real time (e.g., Cisek, 2007; Kelso, 1995; Port & van Gelder, 1995; Rogers & McClelland, 2004; Spivey, 2007; Spivey & Dale, 2004, 2006). More basically, the results show that, as ready and rapid as they may be (Macrae & Bodenhausen, 2000), our construals of others are the result of an interactive, temporally dynamic person perception process (Freeman et al., 2008).

Prior studies have also suggested continuous flow between the neural subsystems for perception and action. However, these studies have relied on indirect behavioral evidence (e.g., Abrams & Balota, 1991; Finkbeiner et al., 2008; Freeman et al., 2008; Freeman et al., 2010b; Miller & Ulrich, 2003; Osman, Kornblum, & Meyer, 1986; Song & Nakayama, 2009; Spivey, Grosjean, & Knoblich, 2005), whereas the neurophysiological evidence comes from studies involving low-level perceptual decisions (e.g., perceptions of shape, size, or motion of dots or letters) coupled with saccadic eye movements in monkeys (e.g., Gold & Shadlen, 2001; Kim & Shadlen, 1999) and hand movements in humans (e.g., Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Miller & Hackley, 1992). Here we extend this research by providing neural evidence for continuous flow between perception and action in a task involving higher-level social decisions (i.e., perception of sex-category). Importantly, the more complex decisions about sex-category in Study 1 were semantic in nature, which involved cognitive competition (Freeman et al., 2008)—a competition we found to continuously extend into the motor system.

Such a finding provides a unique contribution to this body of work on continuous-flow and gradual-accumulation effects in perception and action by extending it to higher-level semantic processing (i.e., categorizing sex, rather than perceiving visual shape/size/motion), in addition to extending it into the domain of a social encounter.

Prior studies investigating the ERP correlates of social categorization have reported larger P200s in response to male rather than female faces and larger N200s in response to female rather than male faces, among other attentional differences to various categories (Ito & Urland, 2003, 2005; Willadsen-Jenson & Ito, 2006). Other studies have examined the role of relatively early components in basic visual encoding of social category information (Freeman, Ambady, & Holcomb, 2010a)[3] or examined stereotype-driven response conflict during social categorization using the LRP (Bartholow & Dickter, 2008). Another study reported that explicit (relative to implicit) sex categorization processing elicits a centro-parietal positivity between 140 and 190 ms and a more posterior negativity between 200 and 250 ms (Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000). The N300/N400 components' modulation by sex-typicality in Study 1, however, provides a neural correlate of social categorization "beyond" a visual level. Rather, it provides a neural correlate of the real-time accrual of knowledge about a person's sex. Future studies might use a similar typical/atypical manipulation to reveal the neural temporal dynamics of building other types of knowledge derived from faces, such as race, age, emotional state, among other possibilities.

The present findings may also have implications for theories positing the coextension of social and motor processes (Knoblich & Sebanz, 2008) and the embodied nature of social cognition more generally (Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005). For instance, if participants make an approach-related flexion with their arm while looking at Chinese letter symbols, the symbols are evaluated more favorably than when participants make an arm extension associated with avoidance (Cacioppo, Priester, & Bernston, 1993). Moreover, when participants make a fist, the fist influences the automatic processing of words tied to the concept of power (Schubert, 2004). These findings, among many others, suggest that cognitive representations are not independent of the motor system, but rather integrated with it. The present ERP results contribute to this work by pointing to closely linked, continuous neural interactivity between the cognitive and motor systems that can help account for the cognitive–motor integration

that is required for such embodiment findings to be neurally plausible.

In real-world social encounters, most of the things we see in others' faces are in continuous flux. For instance, we rarely encounter an obvious, static emotional expression. Rather, for just a few fleeting moments, another's face displays slight anger, which then rapidly transitions into some other expression or gesture. By the time we are finished processing that subtle anger, however, there are already hundreds of milliseconds of new visual information that needs to be accrued and dealt with. In real-world person perception, therefore, another's face tends not to fit squarely into any one expression (e.g., angry), but is usually in some state between one interpretable expression and the next, and rarely standing still. Moreover, these ongoing perceptions need to guide our interaction behavior with another person continuously over time. Something apparent on your friend's face elicits a reaction on your face and in your gesturing, which elicits a reaction on your friend's face, and so on and so forth. Ecologically valid person perception does not consist of a staccato series of easily interpretable static face images that elicit particular reactions. Instead, it seems more likely that person perception involves continuous millisecond-by-millisecond updates of facial information, and these updates need to make their way onto the motor system immediately, not once we have 100% finalized the processing of each transient image in a social interaction. The present ERP findings suggest that this sort of dynamic person processing is a strong possibility. They show that the process of person perception immediately shares its ongoing results with the motor cortex to guide action continuously over time. Of course, presenting participants with static face images on a computer screen in a darkened room while recording electrical brain potentials is hardly the ecologically valid person perception scenario that we speculate about here. However, in our view, this makes the present findings all the more striking—that such continuous perceptual–cognitive–motor dynamics may be evidenced by even the most mundane, stationary stimuli of the laboratory.

In sum, here we demonstrate that ongoing results from the perceptual–cognitive processing of another's face are immediately and continuously shared with the motor cortex, while the motor cortex takes those results and simultaneously prepares for action. The brain begins planning to act on information extracted from another's face well before it has completely finished interpreting what it just witnessed, highlighting the dynamic link between person perception and action.

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