



## The neural representation of faces and bodies in motion and at rest



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### ABSTRACT

The neural organization of person processing relies on brain regions functionally selective for faces or bodies, with a subset of these regions preferring moving stimuli. Although the response properties of the individual areas are well established, less is known about the neural response to a whole person in a natural environment. Targeting an area of cortex that spans multiple functionally-selective face and body regions, we examined the relationship among neural activity patterns elicited in response to faces, bodies, and people in static and moving displays. When both stimuli were static or moving, pattern classification analyses indicated highly discriminable responses to faces, bodies, and whole people. Neural discrimination *transferred* in both directions between representations created from moving or static stimuli. It transferred also to stimuli experienced *across* static and dynamic presentations (one static and the other dynamic). In both transfer cases, however, discrimination accuracy decreased relative to the case where the representations were both created and tested with static or moving forms. Next, we examined the relative contribution of activity pattern and response magnitude to discrimination by comparing classifiers that operated with magnitude-normalized scans with classifiers that retained pattern and magnitude information. When both stimuli were moving or static, response magnitude contributed to classification, but the spatially distributed activity pattern accounted for most of the discrimination. Across static and moving presentations, activity pattern accounted completely for the discriminability of neural responses to faces, bodies, and people, with no contribution from response magnitude. Combined, the results indicate redundant and flexible access to person-based shape codes from moving and static presentations. The transfer of shape information across presentation types that preferentially access dorsal and ventral visual processing streams indicates that a common shape code may ground functional divisions in the processing of face and body information.

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### Introduction

Functional neuroimaging studies indicate that high-level visual processing of people is organized around two salient principles. The first is a striking separation in the processing of faces and bodies. Anatomically analogous, but separate, regions of the cortex exhibit functional selectivity for either faces or bodies (cf., Downing and Peelen, 2011). The specialized face regions include the fusiform face area (FFA) (Kanwisher et al., 1997), the occipital face area (OFA) (Gauthier et al., 2000; Puce et al., 1996), and multiple areas along the Superior Temporal Sulcus (STS). The most consistently found face-selective area in the STS is located posteriorly (pSTS) (e.g., Hoffman and Haxby, 2000; Phillips et al., 1997; Puce et al., 1998), but recent studies report face-selective areas in mid- (Pinsk et al., 2009) and anterior STS (Pitcher et al., 2011). For bodies, there are specialized brain regions that include the extrastriate body area (EBA) and fusiform body area (FBA) (cf.,

Downing et al., 2001; Peelen and Downing, 2005; Schwarzlose et al., 2005; Taylor et al., 2007). The selectivity of these areas can be quite specific, with EBA responding more strongly to images of the body with the face occluded than to images of a whole person (Morris et al., 2006). In addition to ventral areas, parts of the STS respond to biological motions of the body in natural and point light displays (Allison et al., 2000; Downing et al., 2006; Geise and Poggio, 2003). For the combination of faces and bodies into “people”, Kaiser et al. (2013) found that responses to whole people in the right fusiform gyrus could be modeled as a linear combination of face- and body-evoked response patterns. They suggest that whole person responses arise from the co-activation of independent face- and body-selective neural populations.

The second organizational principle of person processing distinguishes faces and bodies *in motion*, from those at rest. For faces, Pitcher et al. (2011) provided clear evidence for this functional dissociation by directly comparing the responsiveness of FFA, OFA, and face-selective regions in the STS to moving and static faces. The rFFA and rOFA responded equally well to static and dynamic faces, but a face-selective region in the right pSTS responded three times more strongly to dynamic faces than to static faces. Pitcher et al. (2011) also found a face-selective region in the anterior STS that responded exclusively to dynamic faces. For bodies,

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both EBA and FBA respond strongly to both static and dynamic bodies (Atkinson et al., 2012; Peelen et al., 2006).

The functional selectivity of individual areas for form (e.g., face, body) versus motion, however, can be difficult to discern without comprehensive tests with variable stimuli, compared across multiple regions of interest (ROIs). Peelen et al. (2006) conducted such tests with the goal of disentangling biological motion selectivity and body-, face-, and motion sensitivity. They applied a voxel by voxel pattern analysis in EBA, FBA, hMT+ and FFA and found that biological motion selectivity correlated significantly with body selectivity in all of the ROIs. This indicates that biological motion sensitivity in these areas is driven by form. Moreover, using point-light displays of facial and bodily motions, Atkinson and Adolphs (2011) showed that these motions selectively activate regions of brain functionally defined by their selectivity for static images of faces (FFA) and bodies (EBA). Consistent with these findings, Downing and Peelen (2011) argued that despite the close proximity of EBA to hMT+ (Peelen and Downing, 2007), the body representations in both EBA and FBA are not tuned to respond to body dynamics. Instead, they propose that EBA and FBA create perceptually unelaborated representations of the shape and posture of bodies.

There is long-standing evidence of the importance of the pSTS in representing moving bodies and body parts (Allison et al., 2000). The role of pSTS in encoding actions is supported by comparisons of the responsiveness of the pSTS to the coherence of action sequences. Downing et al. (2006) found that pSTS responded more strongly to meaningful action sequences (movie frames played in sequence) than to incoherent action sequences (movie frames played out of sequence to present disjointed actions). No such advantage for action coherence occurred in either the EBA or FBA. At a higher level of abstraction, theoretical accounts of neural processing distinctions for moving versus static stimuli are consistent with the disparate task requirements for identification and social communication (cf., Haxby et al., 2000; O'Toole et al., 2002, for faces; O'Toole and Roark, 2010, for bodies/people).

To date, much of what is known about the structure of high-level visual processing of people largely comes from reports of differences in the magnitude of neural activation elicited in response to faces or bodies in dynamic versus static displays. Indeed, functional selectivity for a particular stimulus (e.g., face) at a particular cortical location is defined by the difference in the *magnitude* of the neural response to the stimulus category (e.g., face) versus a control (e.g., object). These magnitude contrasts suggest a complex network of specialized brain regions in person processing distributed across the ventral temporal and superior temporal cortex. Although the existence of functionally selective areas is well established, little is known about how the overall system works when a whole person is seen in a natural environment. To approach this larger question, it is necessary to begin to understand patterns of neural activity across an area of the cortex that spans multiple functionally selective neural regions. To this end, we measured and analyzed neural responses evoked simultaneously across a broad area of VT cortex implicated in processing faces, bodies, and objects. To consider the system as a whole, it is also important to bridge the gap between the magnitude-based neural measures that have established the existence of individual face- and body-selective areas and the anatomically distributed patterns of activity involved in the neural coding of people.

The goal of this study is to understand the relationship among neural activity patterns elicited in response to faces, bodies, and people in static and moving displays. We considered these neural activity patterns in combination with the magnitude-based functional selectivity of these areas for particular classes of stimuli. Specifically, we collected functional magnetic resonance imaging (fMRI) data while people viewed static and moving displays of faces, bodies, and people. Next, we used a pattern-based classifier to discriminate the neural activity patterns associated with static versus dynamic information about people (i.e., face, body, person) across a broad network of relevant brain regions. The present study extends beyond face- and body-selective responses to the response of whole system to person moving

in a natural environment. We address three questions. First, how distinct are the patterns of neural activation for faces, bodies, and people elicited from viewing static versus dynamic displays? Second, to what extent does the discriminability of these representations depend on the *pattern* of neural activation across cortical areas versus the *magnitude* of the neural response? Third, to what extent are the representations of faces, bodies, and people created from moving versus static presentations *transferable* across static and dynamic presentations. In other words, if static and dynamic stimuli differentially access functionally selective areas in the dorsal and ventral streams, to what extent do form-based face, body, and person representations retain a common, or at least, redundantly accessible core?

To address these questions, we first implemented pattern-based classifiers aimed at discriminating the neural response patterns for static and dynamic stimuli (faces vs. bodies, faces vs. people, bodies vs. people). These data provide a baseline profile of the separability of the evoked neural activity for shape information about people that is elicited from static and dynamic presentations. The existence of face- and body-selective areas in the VT cortex predicts that responses to faces versus bodies will be discriminable with pattern classification techniques. Here we provide precise quantitative data on the degree of discriminability of these responses using patterns of neural activity as our unit of measure. These patterns span the cortical areas implicated in person processing. This approach allows us to assess the power of a combination of implicated regions for this discrimination problem. We also compare patterns of representations created with moving and static versions of the stimuli.

Second, to dissect out the contributions of the neural activity patterns from the response magnitudes, we compared classifiers that operated with magnitude-normalized scans ("pure pattern classifiers") versus classifiers that retained information both about the spatial outlay of neural activity and the magnitude of response. These data offer insight into the extent to which selective functional preferences for moving versus static faces, bodies, and people contribute to the neural distinctiveness of these form representations.

Third, to assess the transferability of form representations created with static versus dynamic stimuli, we trained classifiers to discriminate either static or moving form contrasts (e.g., faces vs. people). Next, we tested these classifiers on their ability to transfer this discrimination power both *between* and *across* static and dynamic presentation types. In the "between" or *full transfer* case, a classifier trained to discriminate the neural activity elicited in response to static stimuli (e.g., static face vs. static body) was tested on its ability to discriminate the neural activity elicited with moving stimuli (e.g., moving face vs. moving body), and vice versa (train with moving stimuli and test with static stimuli). In the "across" or *partial transfer* case, a classifier trained to discriminate neural activations elicited by moving or static forms was tested on its ability to generalize this discrimination across neural activity generated by a static versus dynamic form (e.g. static face vs. dynamic body). As noted previously, both FFA and OFA respond strongly moving and static faces (Pitcher et al., 2011), just as EBA and FBA respond strongly to static and dynamic bodies (Peelen et al., 2006). These findings predict some degree of transfer between representations established from moving and static stimuli. We provide precise measures of the degree of transferability of patterns of activity across multiple brain areas implicated in person processing. These data are used to evaluate the extent to which the neural similarity spaces are constant across dynamic and static presentations. The transfer conditions provide a means of evaluating the structure of the neural similarity space of representations (cf., Connolly et al., 2012) created from static versus moving stimuli. Combined, the data from these classifier experiments provide a view of the redundancy of neural shape codes created from static and moving faces, bodies, and people.

For all of the analyses, we first report neural discriminability targeting a broad area of the cortex that spanned functionally selective face and body areas in the ventral and temporal cortex (including the

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